PROCEEDINGS

OF THE

AMERICAN PHILOSOPHICAL SOCIETY

HELD AT PHILADELPHIA FOR PROMOTING USEFUL KNOWLEDGE.

VOL. XXXV. AUGUST, 1896. NO. 151.

Stated Meeting, May 15, 1896.

The Treasurer, MR. PRICE, in the Chair.

Present, 52 members.

Minutes of May 1 were read and approved.

Letters of envoy from the Geological Survey of India, Calcutta; Observatoire Physique Central, Société Impériale Russe de Geographie, St. Petersburg, Russia; Societas pro Fauna et Flora Fennica, Helsingfors, Finland; Université Royale, Lund, Sweden; K. Sächsische Gesellschaft der Wissenschaften, Leipzig; Bath and West and Southern Counties Society, Bath, Eng.; Royal Observatory, Greenwich, Eng.; Meteorological Office, R. Statistical Society, London, Eng.; Missouri Geological Survey, Jefferson City.

Letters of acknowledgment from R. Zoologisch Gesellschaft "Natura Artis Magistra," Amsterdam, Netherlands (148); Zoöl. Botan. Society, The Hague, Holland (148); Colonial Museum (148); Fondation de P. Teyler van der Hulst, Harlem, Holland (148, and *Trans.* xvi, 1, 2); Maatschappij der Nederlandsche Letterkunde, Leiden, Holland (148); Université Royale, Lund, Sweden (147); Prof. Japetus Steenstrup, Copenhagen, Denmark (148); Musée Royal d'Histoire Naturelle de Belgique, Bruxelles (148); R. and T. Observatory, Prague, Austria (148); Dr. H. Rollett, Baden bei Wien (143, 146–148); K. K. Central Anstalt. für Meteorologie und Erdmagnetismus

(148); Dr. Aristides Brezina (145); Prof. Gustav Tschermak, Vienna, Austria (142, 144); Anthropologische Gesellschaft, Prof. Dr. Reuleaux, Berlin, Prussia (148); Vogtländische Altertumsforschenden Verein, Hohenleuben, Saxony (148); Dr. O. Böhtlingk, Prof. I. Victor Carus, Leipzig, Saxony (148); K. Sternwarte (148), Dr. Paul Thyse, Munich, Bavaria (147, 148); K. Geodätische Institut, Potsdam, Prussia (148); Institut de France, Dr. E. T. Hamy, Profs. Gaston Maspero, Leon de Rosny, Paris, France (148); Mr. Samuel Timmins, Arley, Coventry, Eng. (148); Profs. C. A. M. Fennell, R. T. Glazebrook, J. P. Postgate, Cambridge, Eng. (148); Phil. and Lit. Society, Leeds, Eng.; Royal Society, Victoria Institute, R. Astronomical Society, R. Meteorological Society, R. Geological Society, Royal Institution, R. Geographical Society, Society of Antiquaries, R. Statistical Society, Sir Henry Bessemer, Col. William Ludlow, Sir James Paget, Prof. W. C. Unwin, London, Eng. (148); Geographical Society, Manchester, Eng. (148); Lit. and Phil. Society, New Castle-on-Tyne, Eng. (148); Radcliffe Observatory, Prof. James Ligge, Oxford, Eng. (148); R. Geological Society of Cornwall, Penzance, Eng. (148); Dr. Isaac Roberts, Starfield, Crowborough, Sussex, Eng. (148); Nat. Hist. and Phil. Society, Belfast, Ireland (148); Royal Society, Prof. James Geikie, Edinburgh, Scotland (148); Society of Natural History, Portland, Me. (148, 149); Mass. Agricultural College, Amherst (149); Prof. Alpheus Hyatt, Dr. Justin Winsor, Cambridge, Mass. (149); Amer. Antiquarian Society, Worcester, Mass. (149); Amer. Mathematical Society (148), Amer. Institute Electrical Engineers, New York, N. Y. (149), Prof. Lyman B. Hall, Haverford, Pa. (149); Prof. John F. Carll, Pleasantville, Pa. (149); Philosophical Society, West Chester, Pa. (148); U. S. Naval Institute, Annapolis, Md. (148, 149); Maryland Historical Society, Baltimore (149); Smithsonian Institution, Washington, D. C. (144, 145, 146); N. C. Experiment Station, Raleigh (149); Ohio State Archæol. and Hist. Society, Columbus (149); Prof. H. T. Eddy, Minneapolis, Minn. (147–149); Kansas Historical Society, Topeka (149); Observatorio Astronómico Mex-

icano, Tambaya, Mexico (149); Rt. Rev. Crescencio Carrillo, Merida, Yucatan (149); Société Scientifique du Chili, Santiago (141).

Letters of acknowledgment (*Transactions*) from the Museum of Comparative Zoölogy, Cambridge, Mass.; Amer. Antiquarian Society, Worcester, Mass.; Yale University, New Haven, Conn.; The Buffalo Library, Buffalo, N. Y.; Historical Society, Astor Library, New York, N. Y.; U. S. Military Academy, West Point, N. Y.; Haverford College, Haverford, Pa.; Academy Nat. Sciences, Historical Society of Pennsylvania, Library Company, Philadelphia (xviii, 3); Johns Hopkins University, Baltimore, Md. (xvi, 2, 3; xvii, 1, 2, 3; xviii, 1, 2, 3).

Accessions to the Library were reported from the Société des Naturalistes, Kieff, Russia; Société des Naturalistes, Moscow, Russia; K. Russische Geog. Gesellschaft, Phys. Central Observatoriums, K. Mineralogische Gesellschaft, St. Petersburg, Russia; Societas pro Fauna et Flora Fennica, Helsingfors, Finland; I. R. Accad. di Scienze, Lettere, etc., Degli Agratis Roveredo, Austria; K. P. Meteorol. Institut, K. Museums für Völkerkunde, Gesellschaft für Anthropologie, Ethnologie, etc.; Prof. A. Bastian, Berlin, Prussia; Direcção Trabalhos Geologicos de Portugal, Lisboa; Instituto y Observatorio de Marina, San Fernando, Spain; Bath and West and Southern Counties Society, Bath, Eng.; Royal Observatory, Greenwich, Eng.; Literary and Philosophical Society, Liverpool, Eng.; Literary and Philosophical Society, Manchester, Eng.; Hon. J. M. Lemoine, Quebec, Canada; Free Library, Boston, Mass.; Zoölogical Society, Mr. William A. Ingham, Philadelphia; Chief of Engineers, Committee to Establish the University of the United States, Department of Labor, Prof. Alexander Graham Bell, Washington, D. C.; Missouri Geological Survey, Jefferson City; University of Michigan, Ann Arbor; Agricultural Experiment Stations, Lafayette, Ind.; Brookings, S. Dak.; Observatorio Meteorol., Leon, Mexico; Direccion General de Estadistica, Guatemala, C. A.; Museo Biblioteca de Filipinas, Manilla.

Dr. Morris, of the Curators, called attention to photographs presented by Mrs. Stevenson of the relics found in Egypt.

Also, on behalf of Robert Patterson Field, he presented a portrait in oil of Dr. Robert M. Patterson.

The Report of Council was read, in which nominations 1332, 1334, 1357, were recommended to be postponed for written information.

The resolution presented at the meeting of March 20 was recommended for approval, amended to read as follows:

Resolved, That papers by non-members presented to the Society shall be read by title only, except when the author is present or by consent of two-thirds the members present.

Prof. A. H. Smyth then read an obituary notice of Henry Phillips, Jr.

The stated business being the election of members, Secretary DuBois and Dr. Hays were made Tellers. The names were read and spoken to and the ballots cast.

The following papers were then read by title and referred to the Secretaries:

"Second Contribution to the History of the Cotylosauria" by E. D. Cope; "Sixth Contribution to the Knowledge of the Marine Miocene Fauna," by E. D. Cope; "On Natural Selection and Separation," by Arnold E. Ortman; "Notes on the Osteology of the White River Horses," by Marcus S. Farr.

Dr. Frazer announced that Mr. Barkley had brought from New York specimens of results of color photography according to the system of Mr. Joly, and had placed them in Mr. Sachse's hands.

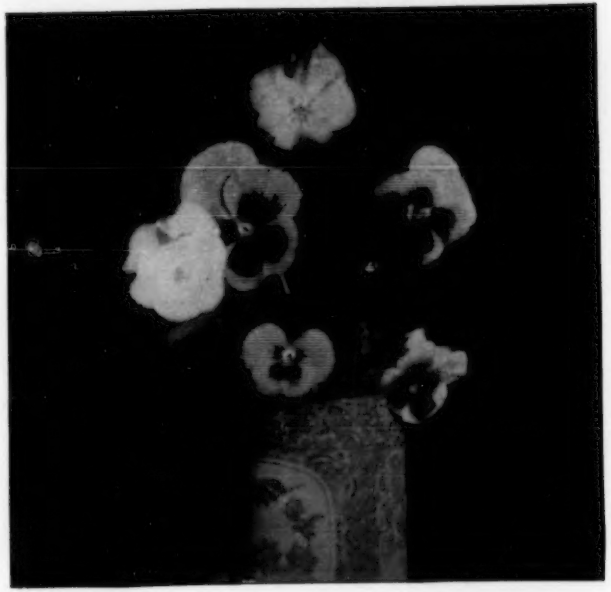
Mr. Sachse then explained the system and exhibited the specimens.

Dr. Frazer then advocated the reproduction in *facsimile* of our signature book for distribution among the members, and the matter was referred to the Secretaries with power to act.

The Tellers reported the result of the ballot, and the following were declared elected:

2282. Edward S. Dana, New Haven, Conn.

NEGATIVE.



POSITIVE.

PRINTS ILLUSTRATING THE JOLY PROCESS.

2283. C. Hanford Henderson, Ph.D., Philadelphia.
2284. Chas. Sedgwick Minot, Harvard Univ., Mass.
2285. L. H. Bailey, Ithaca, N. Y.
2286. Wm. H. Welch, M.D., Baltimore, Md.
2287. T. Mitchell Prudden, M.D., New York City.
2288. John Trowbridge, Harvard Univ., Mass.
2289. Nikola Tesla, New York City.
2290. Arthur W. Wright, Ph.D., New Haven, Conn.
2291. Prof. Henry A. Rowland, Baltimore, Md.
2292. Prof. Arthur W. Goodspeed, Philadelphia.
2293. Prof. Michael I. Pupin, New York City.
2294. Thos. A. Edison, Orange, N. J.
2295. Edw. C. Pickering, Cambridge, Mass.
2296. Frank H. Cushing, Washington, D. C.

The Joly Process of Color Photography.

By Julius F. Sachse.

(*Read before the American Philosophical Society, May 15, 1896.*)

I have the honor to present to your notice this evening, by courtesy of Mr. Richard Barkley, of New York, a series of specimens illustrating the so-called "Joly" process of color-photography.

They are the same as were lately shown before the Royal Society of England, and excited considerable attention.

This process, although it depends upon the three primary color sensations, differs materially from all others thus far brought to the notice of the public, because but a single photographic manipulation is required, and no apparatus is needed other than such as is used in ordinary every-day photography.

This process consists in making a negative through a closely-lined screen, ruled in three colors, viz., orange, yellow-green and blue-violet. The screens used in the specimens here shown were made with an ordinary ruling pen, such as is used by draughtsmen, and the lines number about two hundred to the inch. A finer ruling in the future will make the lines which we now see in the specimens before us less prominent.

It will be noticed that Prof. Joly, in his "taking" screen, which is here before you, has substituted, for the usually accepted primary color

sensations, red, green, blue, the colors orange, yellow-green and blue-violet. Experience has taught him that not only were the former colors unsuitable for the purpose, but that to reproduce the effect of natural colors, a somewhat different screen must be used over the resultant positive image. For this purpose Prof. Joly rules a screen in pure red, green and blue-violet. This he calls his viewing screen.

[For the red-selecting lines of the "taking" screen, Prof. Joly uses a spectrum color, such as that to be found at one-sixth of the distance from the line D to the line C; for the green-selecting lines he uses a color corresponding to that of the spectrum at about one-third of the distance from the E line to the D line; and for the blue-violet-selecting lines he uses a color corresponding to the spectrum color near the F line, but toward the G line. On comparison of the "taking" screen with the spectrum, these colors can be called a red-orange, yellow-green, and a violet-blue. For the colors of the "viewing" screen he uses a pure red not far from the C line; a green near the E line; and for the blue-violet lines he takes a spectrum color between G and H, the object being in the "viewing" screen to transmit fundamental color sensations only, and to let the eye do its own mixing; the eye is assisted by the depth of light and shade in the linear areas of the positive; for instance, if the full amount of light of two adjacent red and green lines be transmitted, the eye sees a yellow; if now some of the green be obstructed or shut out by the positive over it, then the eye will see an orange; and if, on the other hand, some red be shut out by the positive, then the eye sees a yellow-green, and it is easy to see that one can run all the colors from pure red to pure green by the varying amounts of the red or green lines shut out by the positive.]

The first specimen we have here is a negative of a china plate and jug, photographed through the "taking" screen.

The next one is a glass positive printed in contact from the above negative. It will be noticed that neither of these specimens differ from ordinary photographic results except that lines due to the use of the screen are somewhat prominent.

The third specimen is a positive similar to the one just shown, placed in register with a "viewing" screen; and by holding it up to the light, and viewing it through the ruled grating, we see the china plate and jug in the bright colors of the original objects.

The next subject is a male portrait from life; this illustrates the possibility of the process in its application to professional portraiture.

We now have a portrait of an "Irish peasant girl," not from life, it is true, but from a water color, which is here before us. The specimen labeled No 7 is placed in contact with a "viewing" screen. The original is here offered for comparison, so that you may judge of the fidelity of the reproduction to the colors of the original. To prove the correctness of his theory, Prof. Joly here presents another specimen of the same subject, No. 12. This is taken and placed in contact with the same

("taking") screen. The great difference and the falsity of the color rendering will at once be noted by comparison with the original.

The next specimen is perhaps the most interesting one of all, on account of being an almost instantaneous picture.* It represents a military band in the Park of Trinity College, Dublin. It will be noted that the bright reds of the uniform coats are exceptionally well rendered. Further, this example indicates a possible application of this method of color reproduction to snap-shot photography.

I now wish to call your attention to an interesting feature of this process, viz., the necessity for having the photograph and screen in exact register, and viewing it in a normal position. Viewed direct, this transparency shows the colors of nature: the brilliant red hue of the coats is especially noticeable. Now if we turn the transparency so as to view it at a slight angle, we at once note a change of the colors, and, in this particular instance, an apparent change of the nationality of the subjects: in place of English soldiers in bright red coats, we see a body of men dressed in brilliant green: in short, the Englishman appears to have been turned into an Irishman of the most pronounced type.

The next subject is a perfect representation of a green fluorescent bowl made of uranium glass.

We now come to another interesting specimen—a photograph of a bunch of wall flowers, executed in two color sensations only, viz., the red and green sensations. This picture derives an additional interest from the fact that it was made by Prof. Joly at the request of Lord Kelvin, to show the effect of "violet blindness," an extremely rare variety of color-blindness.

I now present to your notice two photographs of the solar spectrum from nature—the first one made through a "taking" screen, and seen through a "viewing" screen, which, as you will perceive, shows some of the principal lines; the other one, both taken and viewed through the "viewing" screen, shows a false color rendition. The yellow passing through the red lines only, is almost entirely represented by pure red. The incorrectness of the result is evident on comparing it with the first specimen or with nature.

I now come to the commercial part of this process. I have here for your inspection a specimen of three-color printing: the original photograph consists of a single negative; the printing was done from three separate half-tone blocks or plates—red, yellow and blue.

This result is obtained by making three positives in the camera from the original negative in the following manner: A special screen is prepared with black lines twice the width of those upon the taking screen, the intervening space being the width of a single line. This screen, when placed in register with the original negative, it will be observed, exposes only every third line of the negative. Now it will be obvious that if this screen be moved the width of a single line before each

*Actual time about three seconds.

exposure, we shall obtain three positives, each showing but one-third of the original negative, and at the same time representing a different color sensation. An ordinary half-tone plate is now made from each positive, in the usual manner, and then printed successively in yellow, red and blue inks, the same as in the ordinary chromo-typographic or three-color process.

In the case under consideration you will note the almost perfect result, without the presence of the objectionable mathematical cross-line hatch-work.

This latter adaptation of the Joly process, I am informed, is the invention of two young men in this country; and should it prove practical and give certain results, it will without doubt be a great step forward in chromo-typography, and also have commercial value.

It is a curious fact that the foundations of the interesting processes I have described are based, and depend for their ultimate success, upon the ruling machine—an invention of Joseph Saxton, a former member of this Society, specimens of whose early photo-mechanical reproductions, made in 1841, are still in our possession.

In conclusion, I will state that the one great advantage which this process seems to offer over other schemes in heliochromy or the three-color process, is the fact that but a single negative is required, which is obtained by the ordinary methods of photography, so that all special or intricate apparatus, with uncertain results, are obviated. It will be further noted that the specimens shown here to-night are among the earliest ones made, with crude appliances as to the ruling of the screens and the pigments.

---

*Second Contribution to the History of the Cotylosauria.**

By E. D. Cope.

(*Read before the American Philosophical Society, May 15, 1896.*)

The examination of new material derived from the Permian formation of Texas enables me to make some important additions to the knowledge of the Cotylosaurian Reptilia, as set forth in my synopsis published in these PROCEEDINGS for November, 1895 (p. 437).

In the first place, I have to describe a type new to the order, and which resembles nothing hitherto found in the Permian beds of North America, or apparently elsewhere. It must be referred to a new family with the following name and characters.

* Read before the U. S. National Academy of Sciences, April, 1896.

OTOCŒLIDÆ.

Posterior border of temporal roof excavated laterally by the meatus auditorius externus. Teeth present in a single row, not transversely expanded. Ribs immediately overlaid by parallel transverse dermoössifications which form a carapace.

In the presence of the meatus auditorius this family differs from the other members of the Cotylosauria. In the latter the vestibular space is enclosed by the lateral part of the temporal roof, and has no distal inferior bounding wall. The meatus results in the Otocœlidæ not merely from the excavation of this roof but also from the excavation of the posterior border of the suspensorium. In Conodectes this excavation is not great, but in Otocœlus it is very considerable, the proximal extremity of the suspensorium having the anterior position seen in the Loricata and Testudinata. It resembles the quadrate of the latter order in the decurvature of the proximal extremity into a descending hook, which partially bounds the meatus posteriorly.

This meatal excavation constitutes an approximation in the Cotylosauria to other and later orders of Reptilia, where it is nearly universal. It is interesting to observe that it precedes in time the division of the roof into longitudinal bars by perforation, in the series of which the Otocœlidæ form a part. This fact renders it probable that it is from this family that the order of the Testudinata has descended. It may also be found that the Pseudosuchia have the same origin. The carapace of the Otocœlidæ approaches nearly that of the genus Typothorax* Cope, of the Trias; where each rib is expanded, and bears above it a distinct dermosseous band of equal width, with a sculptured surface. This genus probably belongs to the Pseudosuchia, whose type genus Aëtosaurus Fraas, has a carapace consisting of transverse bands of osseous plates in mutual contact. The transverse segmentation of the carapacial bands of Otocœlus would produce such a structure. The same character is found in the genus Episcoposaurus Cope of the Trias, where the cranium is unknown. A reduction of the number of the transverse bands of the Otocœlidæ would approximate the carapace to that of the Testudinata. The arrangement of the clavicles and episternum is quite like that of the corresponding elements in the anterior lobe of the plastron in the tortoises. The median and posterior part of the abdominal wall of the Otocœlidæ is unknown. The teeth are quite insignificant,

*In the last edition of Dana's *Geology*, 1895, p. 758, it is inaccurately stated that "A large Crocodilian of the genus Belodon has been described by Cope . . . . under the name of *Typothorax coccinarum*." The fact is, that two animals were included in the description, which I afterwards determined to belong to different genera. The one for which I reserved the name Typothorax does not belong to the genus Belodon. See *Proc. Amer. Philos. Soc.*, 1887, p. 200, Plate I, where the genus and species are defined. Recently Marsh has described (*Amer. Journ. Sci. Arts*, July, 1896, p. 61) the cast of a similar reptile from the Trias of Connecticut, to which he gives the name *Stegomus arcuatus*. He does not distinguish the supposed new genus Stegomus from Typothorax.

PROC. AMER. PHILOS. SOC. XXXV. 151. P. PRINTED AUGUST 12, 1896.

and their loss would bring us again to the Testudinata type. Their implantation in deep alveoli is reptilian in character.

I have pointed out that the notch in the posterior border of the cranial table in the stegocephalous Batrachia was probably covered by a membranum tympani, since the stapes terminates there. This notch is the first appearance of a meatus auditorius in the Vertebrata, and it is not present in all Stegocephalia. It seems that the members of the Cotylosauria differ among themselves similarly, some presenting the meatus, and others lacking it. In Conodectes the character approaches that of the Stegocephalia more nearly than it does in Otocœlus.

In the *American Naturalist* for 1885, p. 247, I published the conclusion that the Testudinata were descended from the Theromora. In my system at that time the Theromora included the Cotylosauria. In 1892 (*Trans. Amer. Philos. Soc.*, p. 24), I distinguished the Cotylosauria as the primitive source of the Testudinata. The discovery of the Otocœlidæ renders it almost certain that this anticipation was correct.

In this family the slight posterior concavity of the quadrate region of the Diadectidæ is extended forwards to a great distance, and the osseous tympanum is produced further outwards. The position of the parts is different from that which is characteristic of the Stegocephalia, where the tympanic notch, when present, is superior, owing to the much greater length of the suspensorium. The dental characters also distinguish this family from the Diadectidæ. No ossicula auditus were found in the tympanic cavity.

Two genera of this family are known, and are characterized as follows:

Mandible articulated much anterior to cranial border; nostrils opening vertically..... *Otocœlus* Cope.
Mandible articulated posteriorly and on line of posterior border of skull; nostrils opening horizontally..... *Conodectes* Cope.

Two species of Otocœlus and one of Conodectes are known from the Permian bed.

OTOCŒLUS TESTUDINEUS, *Amer. Naturalist*, 1896, 399.

Char. gen.—Teeth with simple subconic crowns. Mandibular ramus not produced posterior to quadrate. Superior cranial bones strongly sculptured.

This genus is established on a skull from which the muzzle anterior to the orbits has been broken off. On its under side, pushed forwards out of place, are a considerable part of the shoulder-girdle, the head of the humerus and a bone of the forearm. On another block, which was found with it, is a part of the carapace, two vertebræ, numerous ribs and both hind legs, lacking the tarsus and digits. The legs and vertebræ were not found attached to the foreleg and the skull, but the actual contact of the corresponding parts is found in the type specimen of another species, the *O. mimeticus*.

There is considerable resemblance between several parts of this animal and those of the stegocephalian Batrachia. This is seen in the forms of the femur and of the shoulder-girdle, which are similar to those which I have referred to Eryops. The close approximation of the huge auricular meatus to the orbit is only seen elsewhere in the anurous Batrachia. The teeth on the other hand are of strictly reptilian type in their mode of implantation, and the lack of dentinal inflections distinguishes them from those of many of the genera of Stegocephalia. There is nothing in the shoulder-girdle to distinguish it from the Cotylosauria, and the humerus so far as preserved is of the type of that order. It is impossible to get at the occipital condyles without destroying important parts of the specimen. The vertebræ are amphicœlous.

It is probable that in life the species of this genus had an enormous tympanic drum.

The tabular part of the skull is large as compared with the facial part. Its posterior border is broken in the *O. testudineus*, but it is continued to a transverse line posterior to the auditory meatus. It was not probably produced into horn-like processes. The suspensorial part of the quadrate is directed posteriorly below. The mandibular ramus has a horizontal expansion of the inner side just anterior to the short angle.

The clavicles have the distal expansion overlapping the episternum characteristic of the order. The shaft makes an obtuse angle with the expanded portion, and is compressed. Its proximal extremity is expanded into a rounded disc, whose plane is horizontal and at right angles to that of the shaft. Between the shaft and the mandibular angle the edge of the pterygoid is visible. The episternum has the posterior part broken off. The part preserved is a transverse plate, which has, like the clavicles, a smooth surface. The scapula lacks the proximal end. Distally it presents a strong longitudinal ridge which extends to the coracoid. Anteriorly the shaft expands into a procoracoid laminar extension in its plane. The coracoid is small and has a convex internal border, which is not notched as in the Pelycosauria. It may be coössified with the scapula. The humerus has a greatly expanded head and a narrow shaft.

The femur is longer than the tibia, and displays the condyles characteristic of the Cotylosauria and Pelycosauria. They are unequally produced posteriorly. There is a long and strong anterior crest.

Two vertebral centra are only moderately well preserved. They are probably anterior dorsals. They are wider than long and are separated by a large and protuberant intercentrum. A free intercentrum of the same shape lies at one side. It is probable that a rather short neural spine rises to the inferior side of the carapace. Only the part next the carapace can be seen in the specimen.

The ribs are much expanded, but do not touch each other. The carapacial bands alternate with them above, resting on their adjacent edges and separated by narrow interspaces. Towards the supposed

anterior part, the superior costal surfaces rise between the carapacial bands to the plane of the latter, forming a closer surface than posteriorly.

This genus forms a remarkable example of homoplastic resemblance to the rhachitomous genus Dissorhophus, which I described in the *American Naturalist* for November, 1895. The superficial resemblance is very great, and it is only after an examination of the constitution of the carapace that the difference of this part of the structure in the two genera is observed. In the batrachian genus the ribs are free from and not in contact with the carapace, and the inferior stratum of the latter consists of the expanded neural spines. (See Plate X.)

Char. specif.—Muzzle very short and broadly rounded. Top of head between and posterior to orbits flat. Orbits directed principally upwards. Intertympanic width 2.5 times interorbital width. Table of skull posterior to orbits about as long as wide. Postorbital width (longitudinal) half as great as interorbital width, which is equal transverse diameter of orbit. Long diameter of orbit obliquely directed outwards and forwards. Malar bar narrow. Quadratojugal surface posteriorly overhanging border of mandible a little, and these contracted to an apex overhanging angle of mandible posteriorly. Mandibular angle undivided. The superior surfaces of the skull have a strongly impressed honeycomb sculpture, the ridges between the pits being frequently interrupted. The sculpture extends to the inferior border of the mandible. The pits average 2 mm. in diameter. The sculpture is present on the external surface of the posttympanic hook, where the decurved border is concave. The median parts of the frontal and parietal bones are smooth, but whether this is normal or is the result of weathering I do not know.

The mandibular ramus presents, a short distance anterior to the angle, a horizontal expansion with convex border directed inwards and in contact with the pterygoid.

The crowns of the teeth are acute and smooth. They overlap the edge of the lower jaw and are separated by interspaces equal to their own diameter. They are of quite small size.

The articular face of the humerus extends downwards on the inner border of the head; perhaps it is restricted to this part of the latter. The section of the shaft is semicircular.

The fragment which contains the vertebræ, hind leg and carapace, does not form a fit with any fractured face of the mass containing the skull. As, however, everything about the two blocks is harmonious, and as they were found close together, I have no doubt of their pertinence to the same skeleton. The second block is split longitudinally, so that only one-half of the carapace is preserved; but at the supposed proximal end enough of the middle portion remains to include the two vertebræ already described. A portion of one hind leg, including the distal part of the femur with the tibia and fibula, lie over the carapace

externally, while the three principal elements of the other leg lie on the inferior side of the carapace. Both legs are extended in the same direction, *i. e.*, forwards.

The shaft of the femur has a triangular section, the external face concave owing to the prominence of the anterior crest. The external condyle is produced further posteriorly than the internal, and is a continuation of the general distal surface and is not reflected on the posterior face as in so many of the Pelycosauria. The anterior face is flat above and shallowly concave at the condylar border below. The head of the tibia is expanded and the shaft narrowed, as in Pelycosauria. It is straight, while the fibula presents towards it a concave outline; and the two extremities of the latter are about equally expanded.

The surfaces of the vertebral centra are slightly concave anteroposteriorly. The intercentra are somewhat swollen and knob-like on the inferior face. It is probable that the ribs are less closely adherent to the carapacial bars posteriorly than anteriorly. As already remarked, anteriorly the ribs emerge between the bars to form part of the surface; medially the ribs are below the bars but touch them. Further posteriorly a cross section displays a rib which does not touch a bar, except perhaps at the extremity, as the curvature would indicate; but this part is broken off. The superior surfaces of the carapacial elements are of dense bone marked with coarse and fine fossæ and intervening elevations irregularly distributed.

The size of this animal is about that of the adult of the larger Japanese salamander, Megalobatrachus.

Measurements.

	MM.
Width of skull between meatus auditorius	75
" " " " orbits	31
" " " " orbit and meatus	15
" " orbit, transversely	27
Length of skull above posterior to orbits	65
Depth of malar bone at middle of orbit	12
" " mandible " " " "	14
Length of tooth exterior to alveolus	3
" " clavicle (chord)	78
Widths of clavicle { proximal	22
median	4
distal	21
Transverse diameters humerus { head	35
shaft	5
Length of femur	67
Anteroposterior diameter of femur { proximally	23
distally	20
Length of tibia	51

Measurements.

	MM.
Long diameter of head of do	17
" " " distal end of do	13
Length across ends of six ribs	75
" of part of carapace preserved	105
Width of a posterior carapacial bar	10
" " an anterior " "	8
Diameters of a vertebra { anteroposterior	8
Diameters of a vertebra { transverse	16
Diameters of intercentrum { anteroposterior	6
Diameters of intercentrum { transverse	12

OTOCŒLUS MIMETICUS, sp. nov.

This species is represented by a skull with lower jaw in place, which is connected by a band of matrix to a carapace, and some of the bones of one of the limbs. Greater and smaller parts of thirteen bands of the carapace are preserved.

The skull is short and wide. The superior surface is nearly flat from the posterior border to between the nostrils. The muzzle does not project beyond the mouth border. The orbits and nostrils are not superior in direction, although the superior orbital border is excavated. The nostrils are directed forwards and a little laterally; they are separated by a space equal to the transverse diameter of each. The auricular meatus is large and is directed outwards and not upwards. The posterior hooks of the quadrate project on each side beyond the slightly concave posterior border of the cranial table. Interorbital region flat, considerably wider than the diameter of the orbit.

The carapace commences at a point about as far posterior to the skull as the posterior border of the latter is behind the orbits. The anterior band has an obtuse anterior border like that of the anterior border of the carapace of an armadillo. The bands are gently convex from side to side, and they become narrower anteroposteriorly as we pass backwards. The state of the specimen is such that neither ribs nor vetebræ can be discovered.

As compared with the *O. testudineus* the following differences appear. The table of the skull projects beyond the posterior hook of the quadrate in the former; not so far in the latter. The auricular meatus and orbit present more laterally in the *O. mimeticus*, more vertically in the *O. testudineus*. The size of the two species is not very different.

Measurements.

	MM.
Length of skull on middle line	120
Width " " at posterior border of orbits	90
" " " between orbits	38
" " " " nostrils	22

Measurements.

	MM.
Length of skull (median) to anterior border of orbits	78
Distance from skull to carapace	65
Length of thirteen carapacial bands	155
Anteroposterior diameter of first band	17
" " " seventh band	12

The species is named to express the superficial resemblance to the *Dissorhophus articulatus*.

CONODECTES FAVOSUS, gen. et sp. nov.

Char. gen.—Quadrate bone extending posteriorly so that the mandibular articulation is opposite the posterior border of the cranial table. Meatus auditorius small, connected with a meatal notch. Nostrils directed upwards and a little outwards. Teeth conic, acute, increasing in length to the middle of the maxillary region.

This genus is of much interest, as it displays the character of the family in a less pronounced degree than the genus Octocœlus, and thus approximates more nearly the other forms of Cotylosauria. Its structure illustrates how the meatus auditorius has arisen by the emargination and excavation of the posterior part of the cranial roof of the Cotylosauria. In the other families the access of the internal ear to the external median is closed by the thin temporal roof.

Char. specif.—Established on a cranium with lower jaw in place, which lacks the left half posterior to the orbit, and a piece from the middle of the right side. Both nostrils and a part of the border of the left orbit are preserved, together with the teeth as far posteriorly as the orbit, the premaxillaries imperfectly. A large part of the palate is preserved. The teeth preserved show that the premaxillary teeth are small as in the *Isodectes megalops*, and that they increase in length posteriorly. The maxillopalatines are excavated on the median line so as to present two parallel ridges which continue as far as the posterior border of the internal nares. These ridges probably continue on the palatine bone and they support each a tooth near the posterior extremity. In *Isodectes megalops* the palatines support numerous small teeth on their inner borders. I find no trace of the interior rows of maxillary and mandibular teeth which are characteristic of the Pariotichidæ. Some such teeth may, however, have existed, as a portion of the maxillary bone is wanting from both sides of the skull.

This species is seven or eight times the linear dimensions of the *Isodectes megalops*, and a little smaller than the *Otocœlus testudineus*. The skull is as wide posteriorly as it is long, and is rather depressed, so that the orbits and nares have a vertical as well as a lateral presentation. The muzzle is flat and projects beyond the lower jaw, and it is rounded in outline, and not narrowed and portuberant as in most of the species of Pariotichus. The internareal and interorbital regions are flat. The

narrower brain case is continued between the orbits, and its lateral walls are robust. The palatine bones extend from the maxillaries, and approximate each other nearly on the median line, where they are separated medially by a groove, which becomes wider posteriorly. No teeth can be discerned in the specimen, excepting the large anterior one already mentioned. The surface of the bone is, however, not in good condition. The plate of the pterygoid extends to the jugal on each side, and its posterior border is but little deflected, and is at right angles to the long axis of the skull, with indications of teeth. The posterior branch of the pterygoid is slender. The occipital region is injured. The superior surface of the skull is sculptured, on the posterior frontal region in a coarse honeycomb pattern, the ridges occasionally forming small tubercles.

The teeth are conic, acute, and with a round section. In this respect they differ from those of most of the species of Pariotichus, where the crowns are obtuse. They are rather closely placed, and they increase in length to below the anterior border of the orbit. Their character posterior to this point cannot be ascertained. The single, large palatine tooth is similar to the maxillaries in form, and equals in dimensions the maxillary tooth which is below the posterior border of the nostril. The posterior border of the internal nostril marks a point half way between the posterior border of the anterior nostril and the anterior border of the orbit.

Measurements.	MM.
Total length of skull	158
Width posteriorly	152
Width between nostrils	20
Length from end of muzzle to posterior border of pterygoid plate	103
Width between summits of ridges of vomer	10
Length from posterior border of nostril to anterior border of orbit	41
Length of longest maxillary tooth	10
Diameter of longest maxillary tooth at base	3.5

A part of the muzzle of a second individual was found at the same locality.

DIADECTIDÆ.

I am now able to make some additions to the family of the Diadectidæ. I omitted also in my recent synopsis* of the genera to include the genus Phanerosaurus Von Meyer, from the Permian of Germany, which I had previously referred to this family.† A revision of the species

* *Proc. Amer. Philos. Soc.*, 1895, December, p. 441.
† *Transac. Amer. Philos. Soc.*, 1892, p. 13.

indicates a somewhat different generic reference to that which I have hitherto adopted, as the generic characters have only now become clear to me. The following are the generic characters as I now understand them:

I. Posterior maxillary teeth transverse, depressed, molariform, the heel (external above, internal below) broad and flat.
Skull without dermal or osseous sutures.....*Empedias* Cope.
II. Posterior maxillary teeth compressed, transverse, with non-molariform edge or apex, except on wear.
a Teeth with an external heel, besides the apical cusp.
Cranial bones coössified; dermal scuta few or none.....*Diadectes* Cope.
aa Teeth with a cusp only.
Adult cranium sutureless.....*Bolbodon* Cope.
Cranium with osseous but no dermal sutures.....*Phanerosaurus* V. M.
Cranium with both osseous and dermal sutures.....*Chilonyx* Cope.

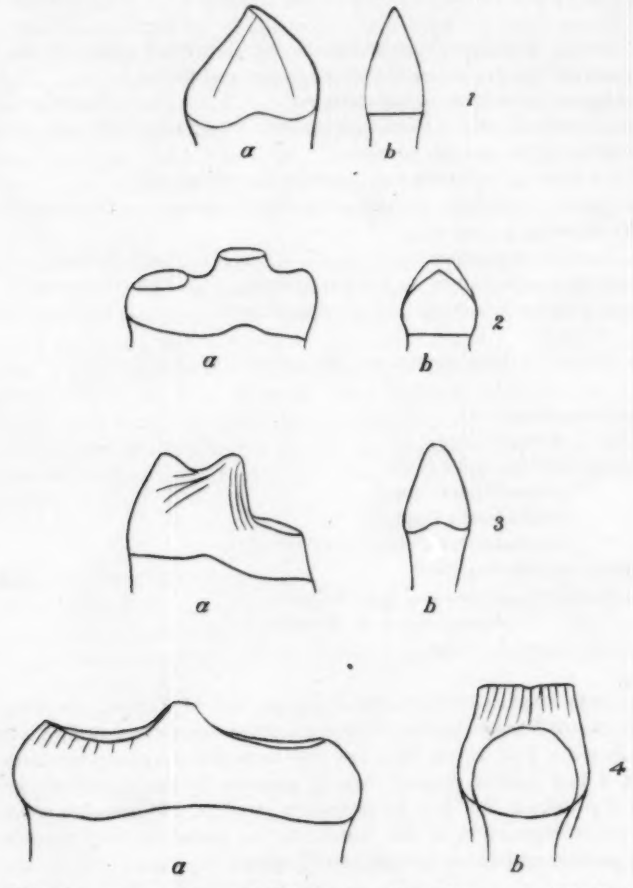
The species of these genera are the following:

Empedias fissus Cope.
" *molaris* Cope.
Diadectes sideropelicus Cope.
" *phaseolinus* Cope.
" *latibuccatus* Cope.
" *biculminatus* Cope.
Bolbodon tenuitectus Cope.
Phanerosaurus naumannii Von Meyer.
" *pugnax* Gein. u. Deichm.
Chilonyx rapidens Cope.

The above species are from the Permian bed of Texas, excepting the two species of Phanerosaurus, which are from the corresponding horizon in Germany. This genus displays the hyposphen-hypantrum articulation in a less perfect degree than it appears in the American genera where it is known, but it is nevertheless present. It presents conspicuously other characters of the family in the broad closely articulating neural arches, and short, robust neural spines

PROC. AMER PHILOS. SOC. XXXV. 151. Q. PRINTED AUGUST 13, 1896.

The molar teeth of three of these genera are represented in the accompanying figures. Nos. 1 and 4 are superior molars, and Nos. 2 and 3 are inferior molars. Their parts are reversed in the two jaws.



1. *Bolbodon tenuitectus.* 2. *Diadectes phaseolinus.* 3. *Diadectes biculminatus.* 4. *Empedias fissus.*

a. Posterior view.
b. End view.

The new forms of the family are as follows:

DIADECTES BICULMINATUS, sp. nov.

As this species is represented by a fragment of a mandible the characters can be drawn from the teeth only. These are remarkable for

their compressed form, and for the unequal elevation of the grinding surface. There is a median cusp much elevated above an external heel, which is at the base of the crown; and there is an internal cusp which is fused to the median cusp, and reaches a similar elevation. It is doubtful whether there are any interalveolar walls, as the teeth are closely placed.

The internal cusp is a little more elevated than the median, and its apex is separated from that of the latter by a shallow notch. The outer wall of the median cusp is vertical, while the inner wall of the inner cusp is convex both vertically and anteroposteriorly. The worn section of the two is unequally dumbbell-shaped. The external face of the median cusp exhibits a median rib, with a groove on each side, besides finer grooves, which are also present on the anterior faces of the crown near the external border. Internal to these, the median cusp sends shallow grooves obliquely inwards and downwards, which do not reach the base of the internal cusp. The transverse diameter of the crowns diminishes gradually posteriorly, so that the alveolus of the last one of the series is small and round.

The groove which separates the teeth from the external parapet of the jaw is half as wide as the width of the molars. Its edge is roughened with projections which separate fossæ and foramina of different sizes. The external surface of the jaw is roughened with innumerable wrinkles and tubercles separated by grooves, fossæ and foramina.

Measurements.	MM.
Length of series of nine teeth	46
Width of crown of largest molar	13
Elevation of external heel	5
" " internal cusp	11
Anteroposterior diameter	5
Width of mandibular ramus at do.	26

The specimen by which this species is known was found by Mr. J. C. Isaac in 1878. It is the "No. 2" of my description of *Diadectes sideropelicus* of the *Proc. Amer. Philos. Soc.*, 1878, p. 505.

DIADECTES SIDEROPELICUS Cope, *loc. cit.*

This species is represented by a left maxillary bone which contains three molar teeth in place and spaces for five or six others. A simple tooth at its anterior part is larger than is usual in the species of this family. I have accordingly defined the genus Diadectes as characterized by the presence of a canine tooth. It is, however, not possible to determine whether the other simple teeth may not have been of equal proportions, as they are represented by alveoli in the specimen. I therefore define the genus by the molar characters, which are distinct. In this respect the species *D. latibuccatus* and *D. phaseolinus* agree with it. In the last-

named the heel of the molars is larger than in the two others, approaching remotely the genus Empedias. The *D. latibuccatus* differs from the *D. sideropelicus* in the smaller number of molar teeth, and smaller and more numerous caniniform teeth.

BOLBODON TENUITECTUS, gen. et sp. nov.

Char. gen.—Molar teeth without external heel, and with one median cusp. Cranial bones coössified; no grooves indicating the sutures of dermal scuta. Internal borders of palatine bones in mutual contact, and dentigerous.

The dentition of this genus is not different from that of Phanerosaurus, as described and figured by Geinitz and Deichmüller.* In that genus, according to these authors, the cranial elements are distinct, the sutures being persistent. In Bolbodon the cranial elements are entirely coössified, excepting only the tabular bone, which is distinguishable. The nostril is large, and a turbinal bone is visible within it as in Pariotichus. The lateral and inferior bones of the brain case, and the mandible, are not preserved.

Char. specif.—This species is represented by a portion of the cranium, which includes nearly the entire right side, and a portion of the median part of the superior wall from the tabular border to the premaxillary inclusive. The vomer and the middle portions of the palatines, with the right premaxillary and maxillary bones, are preserved.

From the middle line at the apex of the vomer to the posterior extremity of the maxillary bone there are alveoli for seventeen teeth. Of these six only are occupied by teeth, which are numbers 5, 7, 10, 12, 13, 16. Of these only numbers 5, 13 and 16 have perfect crowns. The skull has been somewhat distorted by pressure, so that the longer axis of the roots and crowns are somewhat oblique to their correct positions. The roots of numbers 5 and 7 are wide-oval in section, and the long axis becomes longer posteriorly up to the number 16, in which it is a little contracted, and where the entire dimensions are smaller. The crown of number 5 is caniniform and acute, is curved backwards as to its anterior face, and has a worn posterointernal face due to the opposing tooth of the inferior series. In number 13 the crown is much more expanded transversely, and the external vertical border is convex medially and incurved above and below. Curved shallow grooves radiate from the external apex downwards and inwards. The crown of the sixteenth tooth is cordiform, with the acute apex upwards. Shallow grooves descend from the latter. Like the maxillary teeth the palatines are widely spaced. The sections of their crowns are a wide oval placed longitudinally; apices lost.

The nostril is large and is rounded subquadrate. The orbit is large and is subround, and its border is not notched as in the *Diadectes latibuccatus*, nor the superior border depressed as in *D. phaseolinus*. The

* *Mittheilungen min.-geol. u. præhist. Museum of Dresden*, 1882, p. 10.

interorbital space is gently convex, and is wider than the diameter of the eye, but how much wider the state of the specimen leaves uncertain. The jugal bone is quite narrow below the orbit, its vertical diameter equaling two-fifths that of the latter. The surface of the cranium is rather minutely wrinkled, and does not display the grooves seen in the *Diadectes latibuccatus*. The tabular bone forms a rounded and narrowed cap of the posterolateral angle of the skull, and is much less prominent than in the genus Chilonyx, but more so than in Diadectes, where it is not distinguishable by suture.

Measurements.	MM.
Total length of cranium from premaxillary border to os tabulare inclusive	284
Diameters of nostril, vertical	25
Diameters of nostril, transverse	33
Distance from nostril to orbit	78
Diameters of orbit, vertical	53
Diameters of orbit, transverse	54
Interorbital width (posterior to middle)	70
Length of dental series (chord)	150
Diameters m. v, longitudinal	15
Diameters m. v, anteroposterior	7
Diameters m. v, transverse	10
Diameters m. xii, longitudinal	13
Diameters m. xii, anteroposterior	6.5
Diameters m. xii, transverse	13
Diameters m. xvi, longitudinal	10
Diameters m. xvi, anteroposterior	5
Diameters m. xvi, transverse	8.5

The dimensions of this skull are equal to those of the *Diadectes phaseolinus*, and about one-fourth larger than those of the *D. latibuccatus*. The bones of the cranium are thinner and lighter than those of any other species of the family that has come under my observation.

PARIOTICHIDÆ.

PARIOTICHUS ADUNCUS, sp. nov.

Represented by a cranium of which the muzzle and right side, with the right ramus of the mandible, are preserved, together with some other fragments, of one individual; and by a distorted cranium of a second.

The species is intermediate in size and characters between the type of the genus *P. brachyops* and the larger *P. aguti*, besides presenting a number of peculiarities of its own. The elongate maxillary teeth are graded in size to the smaller, and the sixteenth from behind, the largest,

is nearer the anterior border of the orbit than to the nostril. In front of it are three teeth which are preceded by an interval. There are three and perhaps four incisors on each side, of which the external two are small and the internal two very large, the inner the largest. The mandibular teeth increase regularly in length anteriorly. The nostrils are lateral and absolutely terminal. The premaxillary bones are recurved so that the alveolar edge is in vertical line with the posterior border of the nostril. Thus this recurvature exceeds that seen in any other species of the genus, and the symphysis mandibuli is correspondingly posterior. The orbits are larger than in any other species, exceeding the interorbital width considerably, and equaling the length of the muzzle from the orbit to the middle of the nostril. The muzzle is wide above in proportion to its length. It is probable that the width of the skull behind does not exceed the length from the posterior border to the front of the orbit, though this measurement is uncertain owing to the mutilated condition of the right side.

The surface is sculptured with shallow pits separated by rather thick ridges. The nasal bones send back a short angle of the external margin to meet the inferior prefrontal suture, about halfway between the orbit and nostril.

Measurements.	MM.
Length of skull to end of os quadratum	54
" " posterior to orbit	18
" orbit	15
Length from orbit to nostril	12
Width of muzzle at middle	15
" interorbital space	10
" internareal "	8
Length of recurved part of premaxillary	7
" premaxillary I, 1.	5
" longest maxillary tooth	4
Depth of mandible at middle of orbit	6

From the Permian formation of Texas.

? PARIASAURIDÆ.

LABIDOSAURUS HAMATUS Cope, gen. nov. *Pariotichus hamatus* Cope, *Proc. Amer. Philos. Soc.*, 1895, p. 448, Pl. viii, Figs. 1 and 2.

Char. gen.—One series of pleurodont maxillary teeth slightly unequal in size. Internal incisor much enlarged, conic, acute, and directed backwards. No teeth on the maxillopalatines; teeth on the palatines small, subconic, in one row. Nostrils lateral.

Better specimens of the above species show that it has but one row of maxillary teeth, which are pleurodont, so that it is clearly a member of a genus distinct from Pariotichus. If the character I have assigned as

definitive of the Pariotichidæ be the true one, the genus Labidosaurus must be referred to a different one, and I know of no character at present to separate it from the Pariasauridæ of which the known species are so far as known up to the present time restricted to South Africa. It differs from the known genera of that family in the greatly elongate premaxillary teeth, and in the simple conic dental crowns.

Char. specif.—Specimens since received display numerous characteristic peculiarities not preserved in the type. The sculpture of the cranial surfaces is in shallow fossæ with rather thick partitions, of smaller size than in the *Pariotichus aguti*, which resembles it most nearly. Thus there are a dozen ridges between the orbits on the front in the latter, while there are fifteen to seventeen in the *L. hamatus*. The maxillary teeth are relatively smaller than in any of the species of Pariotichus known, and they extend only to below the middle of the orbit. The orbit is subround; in the type it is oval, perhaps owing to pressure. Its diameter is about half the length of the skull, both anterior and posterior to it, and equals the interorbital width. The nostril is anteroposteriorly oval, and the apex of the elongate incisor tooth is below its anterior part. Thus, though the muzzle is more elongate than in any of the species of Pariotichus, it does not project so far beyond the premaxillary border. Length of skull of new specimen 155 mm.

APPENDIX ON A SPECIES OF TRIMERORHACHIS.

TRIMERORHACHIS CONANGULUS, sp. nov.

Size, the least of the species of the genus. Angle of the mandible produced, conic. Orbits rather large, the posterior border nearer the line of the end of the muzzle than to the posterior extremity of the mandibular angle, but not so near as to the posterior border of the tabular bone. External nares half way between orbit and end of muzzle. Interorbital width equal diameter of orbit.

Teeth small, the crowns elongate and acute. Twenty-two may be counted from the posterior end of the series to a point opposite the anterior border of the orbit. A much larger tooth is situated on the external border of the maxillopalatine ("vomer"), a little distance in front of the choanæ, while an equally large one is situated directly on the posterior border of the latter. Another tooth of equal size is situated external to the posterior tooth, near the maxillary border, and the base of a smaller one is visible beneath the two.

The mandibular ramus becomes quite slender anteriorly. Posteriorly, the sutures of the angular, articular, dentary and splenial, are distinct. The symphysis projects beyond and turns up in front of the premaxillary border. The angle projects considerably beyond the quadrate, and is rounded below and at the sides. The extremity is vertically grooved, but whether accidentally or normally I cannot determine.

The elements composing the cranial roof are mostly distinguishable.

The supraoccipitals have considerable extent on the superior face of the skull. The largest bones are the parietals, whose median suture is interrupted by the foramen at about the middle. The next largest bone is the tabular, which extends half the length of the parietal forwards. The supramastoid is pyriform and is rather small, and its anterior angle is wedged in between the posterior parts of the postfrontal and postorbital. The postfrontals separate the frontals from the orbital border. The frontals are distinct, and their posterior border is about in the line of the posterior borders of the orbits. The supratemporal region is injured, and only the suture between the quadratojugal and jugal is visible.

The sculpture consists of radiating ridges from some point in each bone to its circumference. This point may be near the centre or one of the borders of the bone. The ridges may be more or less interrupted and inosculating. They are present on the lower jaw as well as the upper.

Measurements.	MM.
Length of skull on base including symphysis	40
Width of skull at quadrate articulations	36
Length of mandibular angle from do	6
Transverse diameter of orbit	5
Length from posterior border of skull to orbit	18
Width between nostrils	10

From the Permian bed of Texas.

EXPLANATION OF PLATES.

Plate VII.

Otocœlus testudineus Cope; parts of skull and skeleton with carapace, from above; two-thirds natural size.

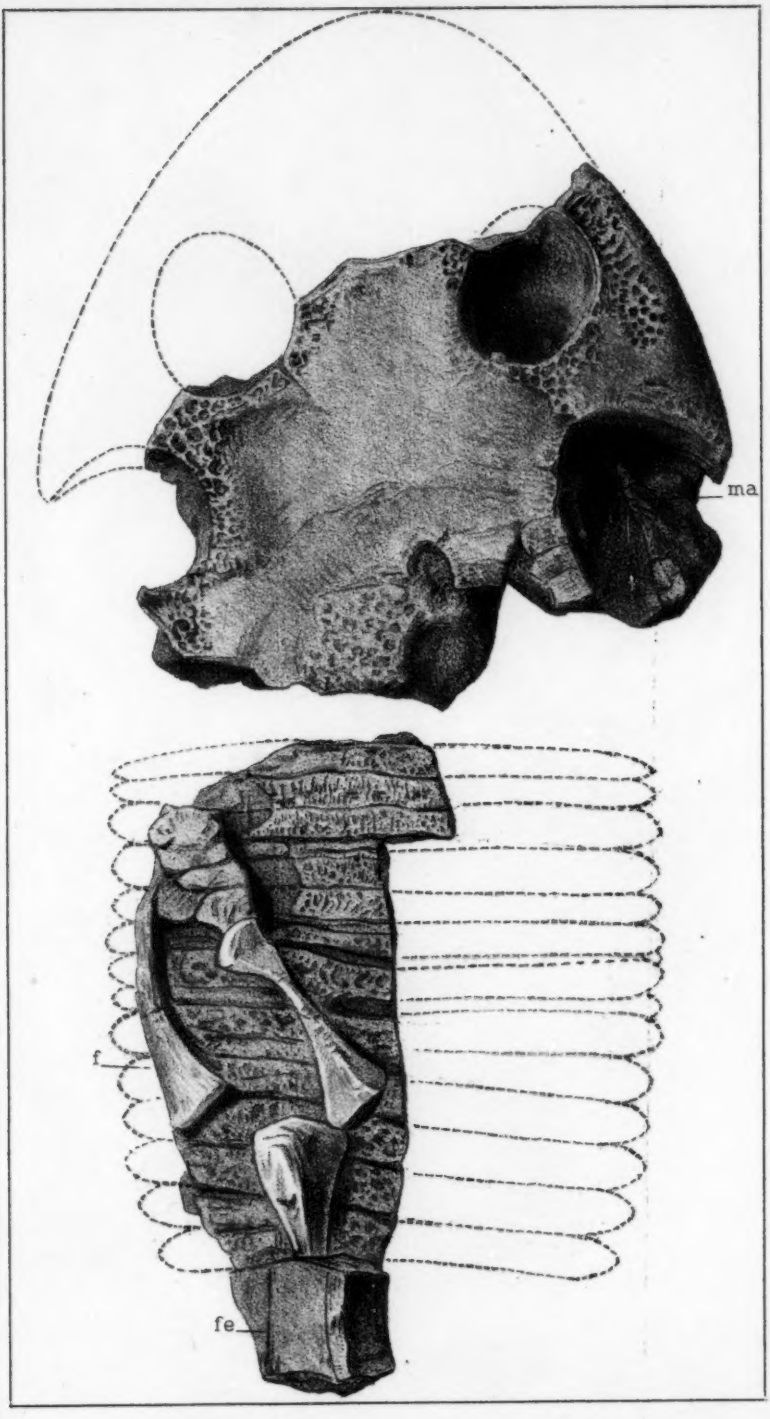
Plate VIII.

Otocœlus testudineus Cope; specimen figured on preceding plate, from below; two-thirds natural size.

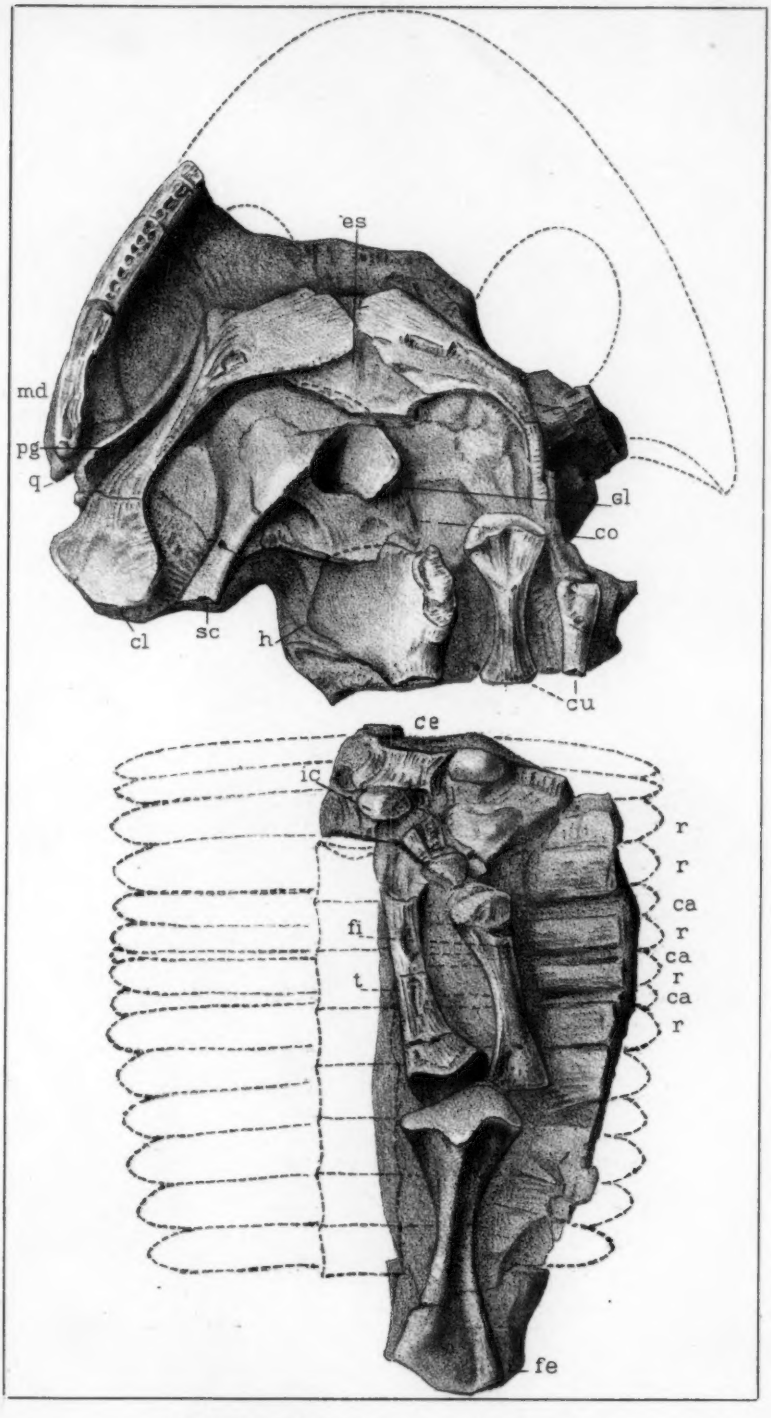
Plate IX.

Fig. 1. *Otocœlus mimeticus* Cope; skull and part of carapace in continuous relation in the matrix, from above; three-fifths natural size.

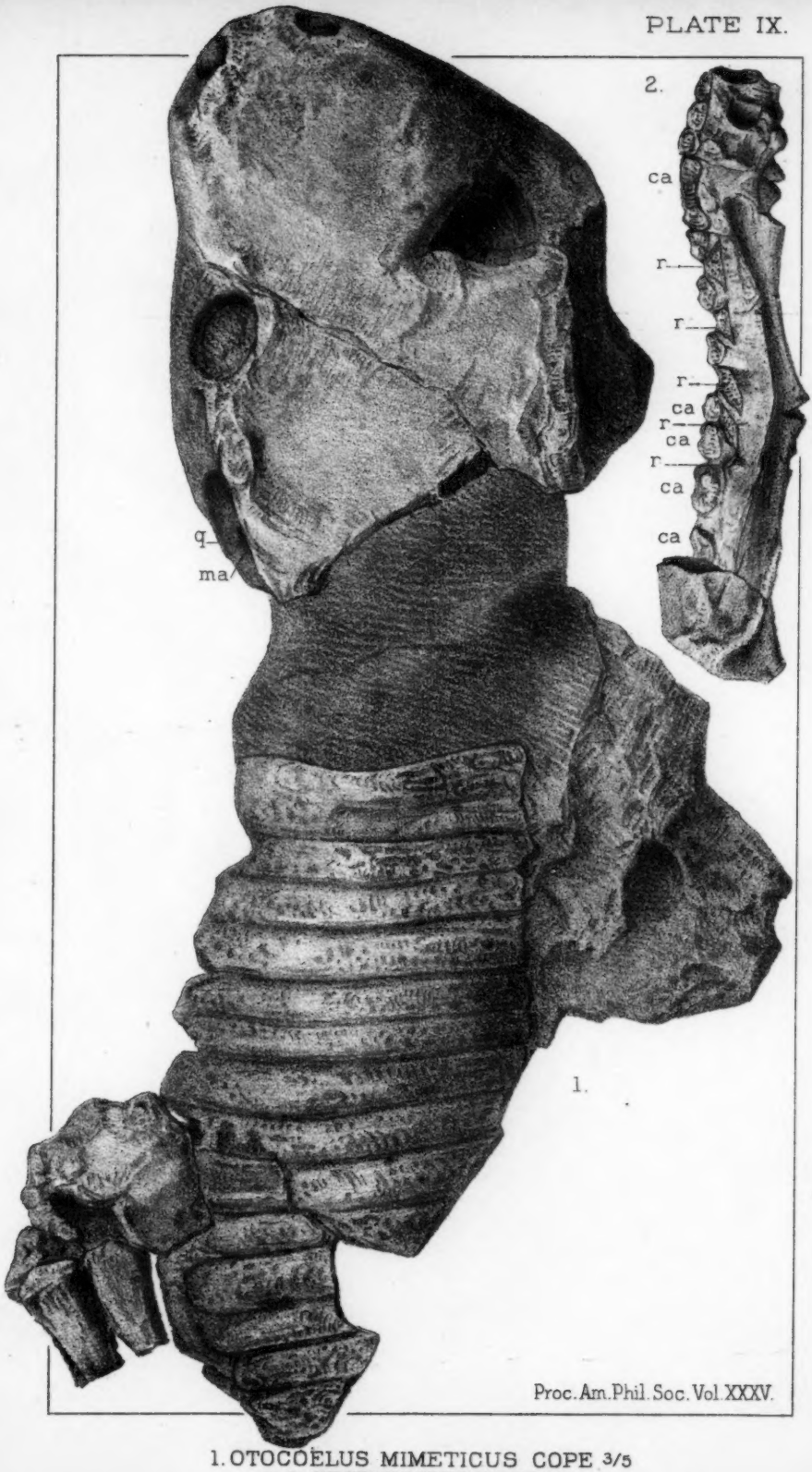
Fig. 2. *Otocœlus testudineus* Cope; broken edge of typical specimen representing sections of ribs and carapacial bands near the vertebral column; two-thirds natural size.



OTOCOELUS TESTUDINEUS COPE 2/3



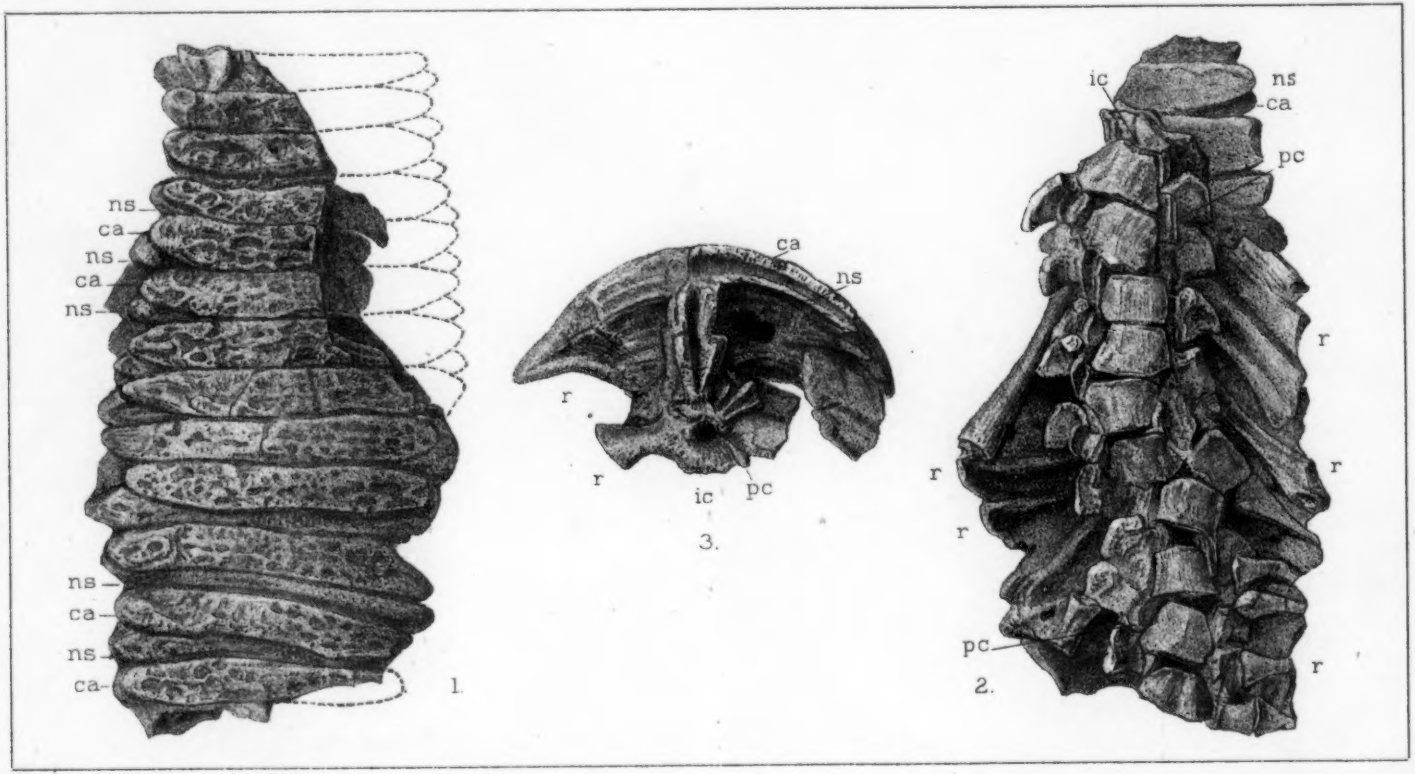
OTOCOELUS TESTUDINEUS COPE 2/3



Proc. Am. Phil. Soc. Vol. XXXV.

1. OTOCOELUS MIMETICUS COPE 3/5
2. O. TESTUDINEUS COPE 2/3

PLATE X.



DISSORHOPHUS ARTICULATUS COPE 5/6

PLATE X.

Dissorhophus articulatus Cope, *American Naturalist*, 1895, p. 998; portion of skeleton, five-sixths natural size.

Fig. 1. Carapace from above.

Fig. 2. Vertebral column ribs and carapace from below; same specimen as Fig. 1.

Fig. 3. Anterior extremity of same specimen.

Lettering.

Q., Quadrate bone; *Md.*, Mandible; *Pg.*, Pterygoid; *MA.*, Meatus auditorius externus; *Cl.*, Clavicle; *Es.*, Episternum; *Sc.*, Scapula; *Co.*, Coracoid; *Gl.*, Glenoid cavity; *H.*, Humerus; *Cu.*, Cubitus; *Ce.*, Centrum; *Ic.*, Intercentrum; *Pc.*, Pleurocentrum; *Ns.*, Neural spine; *R.*, Rib; *Ca.*, Carapace; *Fe.*, Femur; *T.*, Tibia; *Fi.*, Fibula.

Sixth Contribution to the Knowledge of the Marine Miocene Fauna of North America.

By E. D. Cope.

(*Read before the American Philosophical Society, May 15, 1896.*)

The fifth contribution was published in the PROCEEDINGS of the Society for 1895, p. 135, and the fourth in the same for 1870, p. 270.

SYLLOMUS CRISPATUS Cope, gen. et sp. nov.

Char. gen.—Order Testudinata; family probably Cheloniidæ. Costal bones developed beyond rib extremities, and uniting with marginals by suture. Surface sculptured with grooves and ridges. Humerus with entepicondylar foramen enclosed, and flattened shaft. Radial process remote from head.

This is the only definable form of Testudinata yet discovered in the Yorktown bed of the Chesapeake region. It is quite rare, as I have met with it at one time and place only. The carapace is more fully developed than in Chelone and Argillochelys, and it differs from these and from Lytoloma in the sculpture of the surface. From all of these genera and from Peritresius it differs in the union of the marginal bones with the costoids by suture.

A few fragments of a species of Lytoloma have been found in the same formation.

Char. specif.—This tortoise is known to me from two incomplete costal bones and a humerus. One costal fragment is distal, and the other is proximal. The humerus has the deltoid crest broken off at the base.

The carapacial bones are very thin and consist of a thicker superior

dense layer, a light spongy layer, and a very thin inferior dense layer. There were no horny scuta, and it is doubtful whether there were any dermal sutures. The surface is marked with numerous tubercles which are of elongate form, and run in various directions, frequently inosculating and separating generally narrow fossæ. They are finer and more nearly parallel on the distal part of the costal than on the proximal, and they turn at right-angles to the intercostal sutures. The proximal part of the costal is crossed by an angular keel which runs parallel to the middle line of the carapace. It is smooth, interrupting the sculpture. There are therefore two low parallel keels on the superior part of the plastron. Whether there is a median keel cannot be determined, as no vertebral bone is preserved. At one side of this keel (? proximad) is a smooth shallow groove, which may represent the border of a vertebral scutum. Not enough of it is preserved to demonstrate its nature.

The shaft of the humerus is flat in the plane of the distal extremity and is nearly straight, except that it bends a little downwards proximad of the distal extremity of the deltoid crest. The latter descends low on the shaft marking one-third the length. Its inferior portion is recurved inwards towards the head. The long axis of the head is at right angles to that of the shaft. The radial process is prominent, and marks two-fifths the length of the shaft from the head on the internal edge. The straight line of the axis of the humerus reaches the distal extremity between the condyles and the entepicondylar foramen. Thus the condyles are turned slightly ectad. The internal portion of the condyle has a greater anteroposterior diameter than the external, and though the articular surface is convex anteroposteriorly, transversely there are three shallow concavities, one external and two internal. The internal epicondyle is wide and flat, and equals the condyles in transverse diameter. The external epicondyle is little prominent. The entepicondylar canal is oblique, entering nearer the inner margin below, and issuing at about the middle above.

Measurements.	MM.
Proximal width of costal 1	47
Thickness of do. at margin	7
Width of costal 2, at distal end	60
Thickness of do. at distal margin	3
Length of humerus	100
Diameters of head { anteroposterior	32
Diameters of head { transverse	17
Width of humerus distally	41
Transverse extent of condyles	22
Length from radial process to distal end	53

I obtained the specimens above described from a Neocene bed on the Pamunky river, Virginia. It was associated with the *Mesocetus siphunculus* Cope, and various species of Platanistidæ, and a Squalodon.

METOPOCETUS DURINASUS, gen. et sp. nov.

Char. gen.—Lateral occipital crests continuous with anterior temporal crests which diverge forwards. Frontal bone elongate, not covered posteriorly by the maxillary, coössified with the nasals. Nasals short, coössified with each other, not projecting anterior to frontals.

Accompanying the cranial fragment on which this genus is founded is a piece of a premaxillary bone of appropriate size, which presents the character of that of a whalebone whale. The true position of this genus is probably between Cetotherium and Agorophius. It is probably a mysticete which approximates the ancestral zeuglodont type which is represented in our present knowledge by the genus Agorophius. It is connected with Cetotherium by the new genus Cephalotropis, which is described below. The three genera form a group, which may be properly referred to the Balænidæ, which is characterized by the elongation of the frontal and parietal bones on the superior walls of the skull. They differ as follows:

A temporal ridge; maxillaries little produced posteriorly; nasals not produced beyond frontal, coössified with the frontal and with each other.....*Metopocetus* Cope.

A temporal ridge; maxillaries much produced posteriorly; nasals free from frontals and from each other, produced well anteriorly.....*Cephalotropis* Cope

No temporal ridge; maxillaries much produced posteriorly; nasals free from frontals and from each other, well produced forwards.....*Cetotherium* Brandt.

The specimen on which the genus Metopocetus is founded is quite mature so that the sutures are coössified. The frontomaxillary and frontopremaxillary sutures are however distinct, as they appear to me, and they are remarkable for their position. They extend but little posterior to the external nareal openings. The latter are, in relation to the supraoccipital crest, anterior, but in relation to the position of the nasals, posterior. The nasals are short for a Balænid, although they enter wedge-like into the frontals for a considerable distance.

The position of the genera Metopocetus and Cephalotropis may be similar to that of the genera Ulias and Tretulias, which are known from mandibular rami only. One or both of the former may be identical with one or both of the latter; but of this there is as yet no evidence.

Char. specif.—The specimen which represents the *Metopocetus durinasus* is a cranium posterior to the nares, lacking the left exoccipital and squamosal regions, and the right zygomatic process. Both occipital condyles are preserved, and the basicranial region as far as the anterior nares.

The supraoccipital extends well forwards and its lateral crests present a moderate concavity outwards and forwards. Its apex is represented by a semicircular mass, posterior to which it is deeply concave, and the concavity is divided by a longitudinal median crest. The temporal

fossæ approach near together on the median line, forming a short sagittal crest, which is about as wide as it is long. From this the temporal ridges diverge abruptly, and these extend in a nearly straight line forwards, diverging from the line of the axis of the skull at an angle of about twenty-five degrees. Between it and the lateral occipital crest the temporal fossa is concave to the line of the anterior border of the squamosal bone. At the latter point the line of the suture presents an angle, which extends downwards, outwards and forwards. Between it and the posterior temporal crest the surface is concave above.

The exoccipital is flat vertically, and extends a little posterior to the transverse line of the occipital condyles. The postglenoid face of the squamosal is vertical, and it projects laterally beyond the exoccipital. The postglenoid crest is not conspicuous, and the glenoid cavity presents downwards, and very little forwards. The posterior temporal crest bounds a groove of the superior face of the part of the squamosal that lies posterior to it. The latter face is quite wide, and its external bounding angle is a right angle. It is continued as the superior face of the zygomatic process.

The petrous bone has a peculiar form. Its mastoid portion presents externally a nearly discoid outline between the exoccipital and squamosal. Its inferior portion descends as a process which forms the short stem of a half-tubular horizontal portion, which opens downwards and posteriorly, forming a partial meatus auditorius.

The lateral descending borders of the basioccipital are so prominent as to enclose a deep groove between them. The posterior nares are about opposite to the anterior border of the foramen lacerum.

The frontal region at its posterior apex is convex from side to side. As it widens it presents three subequal faces, two lateral and one median. The median plane is separated from the laterals by a shallow groove on each side, which become deeper anteriorly, and turn abruptly outwards at the nareal border. They appear to be the outlines of the nasal bones. Anteriorly the lateral planes become thickened longitudinally just external to these grooves. The entire anterior portion of the external planes is a sutural surface, with longitudinal grooves for a length averaging 40 mm. This surface can relate to nothing but the premaxillary and maxillary elements. This point of attachment is, however, anterior to that of any known genus of Mysticete; and is anterior to that in the *Agorophius pygmæus* Müll. In not extending so far posteriorly as the nasal bones, it leaves the frontals to embrace the latter anteriorly to an unusual extent. This is on the supposition that the indistinct grooves on each side of the middle line really represent the lateral borders of the nasal bones, which is not certain, except as to their anterior portions.

Measurements.	MM.
Width of skull at exoccipitals	406
" " " postglenoid angles	570

Measurements.	MM.
Width of occipital condyles	150
" foramen magnum	65
" sagittal crest	17
" anterior border of nasal bones	90
" skull at sagittal crest	170
" sphenoid at middle of for. lacerum	135
Anteroposterior diameter of glenoid surface	115
Length of nasal canal	250
" from occipital condyles to anterior nares	450
" " foramen magnum to posterior end of sagittal crest (oblique)	210
Length of sagittal crest	15
" from " to anterior nares	195

This specimen was obtained by Prof. Arthur Bibbins from a Miocene marl from near the mouth of the Potomac river, in Maryland. I am under much obligation to the Rev. John T. Goucher, President of the Woman's College, of Baltimore, for the opportunity of studying the specimen, which belongs to that institution.

CEPHALOTROPIS CORONATUS, gen. et sp. nov.

Char. gen.—Parietal bone separating supraoccipital and frontal by a considerable space and presenting a sagittal crest. Frontal extensively overlapped by the maxillaries, premaxillaries and nasals. Nasals elongate, distinct from the adjacent elements. Frontal presenting divergent temporal angles.

This genus differs from Cetotherium in the presence of temporal ridges or angles. It differs from Metopocetus in the free elongate nasal bones.

Char. specif.—The specimen which represents this species is a portion of the cranium which includes the elements which surround the brain except the occipital, the superior part of the latter remaining; together with the posterior parts of the maxillaries, premaxillaries and the greater part of the nasals, and the basisphenoid and presphenoid in part, and a considerable portion of the left temporal. The sutures distinguishing the several elements are distinct, so that the boundaries of the latter can be readily distinguished. In describing this fragment I will compare it especially with the *Metopocetus durinasus* and *Cetotherium megalophysum*, where the corresponding parts are preserved.

The supraoccipital angle is produced further anteriorly than in either of the species named, and the sagittal crest is longer than in either. The summit of the smooth occipital surface forms a transverse border, which cuts off the apex of the occiput, thus bounding posteriorly a triangular area, of which the sides are a little longer than the base. This triangle has a low, median keel, on each side of which the surface is

concave, and is marked with numerous irregular fossæ. The surface has been evidently the seat of the insertion of something; but whether it was entirely of a ligamentous character or whether some tegumentary structure had its basis there I do not know. The superior border of the temporal fossa is regularly concave towards the middle line, and regarding the sagittal crest as restricted to the parietal bone, its truncate edge is wider at the extremities than at the middle. The narrowest portion of the crest is nearer the frontoparietal than the parietoöccipital suture. The temporal ridge is in regular continuation of the edge of the sagittal crest, and becomes transverse in direction towards the orbital border of the frontal bone. This border is broken off.

The vertical temporoparietal suture does not run along a ridge as in the *M. durinasus*, but its superior portion is on a low, obtuse angle. The frontoparietal suture extends posteriorly from the sagittal crest downwards, much posterior to the direction it presents in the *C. megalophysum*, where its direction on each side is a trifle anterior to transverse. Across the front the suture is coarsely serrate, differing from the sutures of the anterior border of the frontal bone, which are closely and deeply interdigitate, as in the *C. megalophysum*. The superficial median part of the frontal is about one-third as long as the corresponding part of the parietal. The nasomaxillary suture with the frontal is short in the transverse direction, not reaching the temporal ridge on each side. The frontomaxillary suture then becomes nearly longitudinal for a distance of 50 mm. and then turns outwards for 25 mm. On the opposite side the posterior border of the maxillary is more oblique, and extends from the transverse median portion divergent from the line of the temporal ridge, forwards and outwards. The latter is probably the normal direction of the suture. The nasal bones are very narrow, but expand gradually anteriorly. They do not terminate posteriorly in an acute angle as they do in the *C. megalophysum* and *M. durinasus* (apparently), but are truncate. The premaxillaries are also narrow at this point. Their posterior extremities are broken off. The glenoid cavity presents downwards. The presphenoid is plane below anteroposteriorly and transversely posteriorly, but is slightly convex below anteriorly. It is hollow.

Measurements.	MM.
Length of supraoccipital triangle to occipitoparietal suture	80
Length of pariëtal on middle line	60
" frontal " " "	25
Width of supraoccipital at base of supraoccipital triangle	124
Width of base of cranium opposite supraoccipital triangle	115
" sagittal crest	18
" nasals at base	28
" " 140 mm. anterior to base	50

In the interstices of the specimen portions of matrix remain which have the color and character of the material of the Yorktown formation. Embedded in this at certain points are fragments of Mollusca of the genera Pecten, Lucina and Turritella. It was probably derived from the Chesapeake region. The fragment belongs to the museum of Johns Hopkins University, of Baltimore, and I am under many obligations to Prof. William B. Clark, State Geologist of Maryland, for the opportunity of studying it.

RHEGNOPSIS PALÆATLANTICUS Leidy. *Balæna palæatlantica, Proceeds. Academy Phila.*, 1851, p. 308. *Balænoptera palæatlantica* Cope, *Proceeds. Academy Phila.*, 1868, p. 193. *Protobalæna palæatlantica* Leidy, Extinct Mamm. Dakota, Nebraska, 1869, p. 440.

The typical and only specimen of this species is a fragment of a lower jaw from the Yorktown bed of S. E. Virginia. Its specific characters differ from those of other Balænidæ referred to in this and preceding papers by me, and it displays in addition a character which Leidy has described, and which is very conspicuous. That is, the presence of a Meckelian fissure, which extends deeply into the mandibular ramus. I agree with Leidy that this feature should be regarded as generic, and so define the genus as follows, under the name Rhegnopsis. Roof of dental canal perforated by gingival tubes; a Meckelian fissure. Dr. Leidy's name Protobalæna is preoccupied by Van Beneden (1867).

CETOTHERIUM LEPTOCENTRUM. *Eschrichtius leptocentrus* Cope, *Proceeds. Academy Phila.*, 1867, p. 147. *Cetotherium leptocentrum* Cope, *American Naturalist*, 1890, p. 616. *Cetotherium crassangulum* Cope, *Proceeds. American Philosophical Society* 1895, p. 148.

After the latest description of this species was published I visited the locality at which it was discovered, in company with Prof. Arthur Bibbins, of Baltimore. I found a part of a mandibular ramus which coincides in all respects so closely with the portions which are still adherent to the skull that I have no doubt that they pertain to the same species, and probably to the same individual. One character in which this fragment agrees with the other portions of the rami is the presence of coarse cancellous bony tissue throughout the gingival dental canal. This reduces the diameter of the latter to that of the large external gingival canals. The form of the middle part of the ramus as indicated by the fragment is very different from that of any other whalebone whale known to me. The internal face is nearly flat and vertical, while the external face is convex only at the superior portion. For a short distance exterior to the superior angle it is subhorizontal; it then gradually decurves, and is then entirely flat to the inferior subacute edge. The section is then subtriangular, with the base superior and the apex inferior. The interior gingival foramina continue very small, and they are not connected by a groove. Distance between two of them,

45 mm. The external foramina are quite large; distance between two of them, 165 mm.

A third cervical vertebra was picked up on the James River, Virginia, by Prof. Bibbins, a few miles below the locality from which the type specimen of the *C. crassangulum* was derived, and kindly presented by him to me. It belongs to an adult animal, and considerable parts of one of the parapophyses and neurapophyses are preserved. The former are directed downwards at an angle of about 25°, and therefore much less steeply than in the *C. cephalus*. The form of the centrum is a transverse parallelogram and therefore similar to that of the two individuals previously described. The diameters are: transverse below middle 140 mm.; vertical 97 mm.; anteroposterior at base 34 mm. The dimensions, while less than those of the type *C. crassangulum*, are appropriate to a smaller individual of that species.

EXPLANATION OF PLATES.

PLATE XI.

Fragmentary crania of Balænidæ of the Yorktown epoch, one-sixth natural size.

Fig. 1. *Cetotherium megalophysum* Cope, from above. Coll. Johns Hopkins University.

Fig. 2. *Cephalotropis coronatus* Cope, from above. Coll. Johns Hopkins University.

Fig. 3. *Metopocetus durinasus* Cope, from above. Coll. Woman's College, Baltimore.

PLATE XII.

Diagrams of sections from near the middle of the mandibular rami of extinct Balænidæ, one-half natural size.

Fig. 1. *Cetotherium leptocentrum* Cope; Virginia.

Fig. 2. *Cetotherium cephalus* Cope; Maryland; section proximad of the middle.

Fig. 3. *Cetotherium cephalus* Cope, same jaw as Fig. 2, distad of the middle.

Fig. 4. *Cetotherium davidsonii* Cope; California.

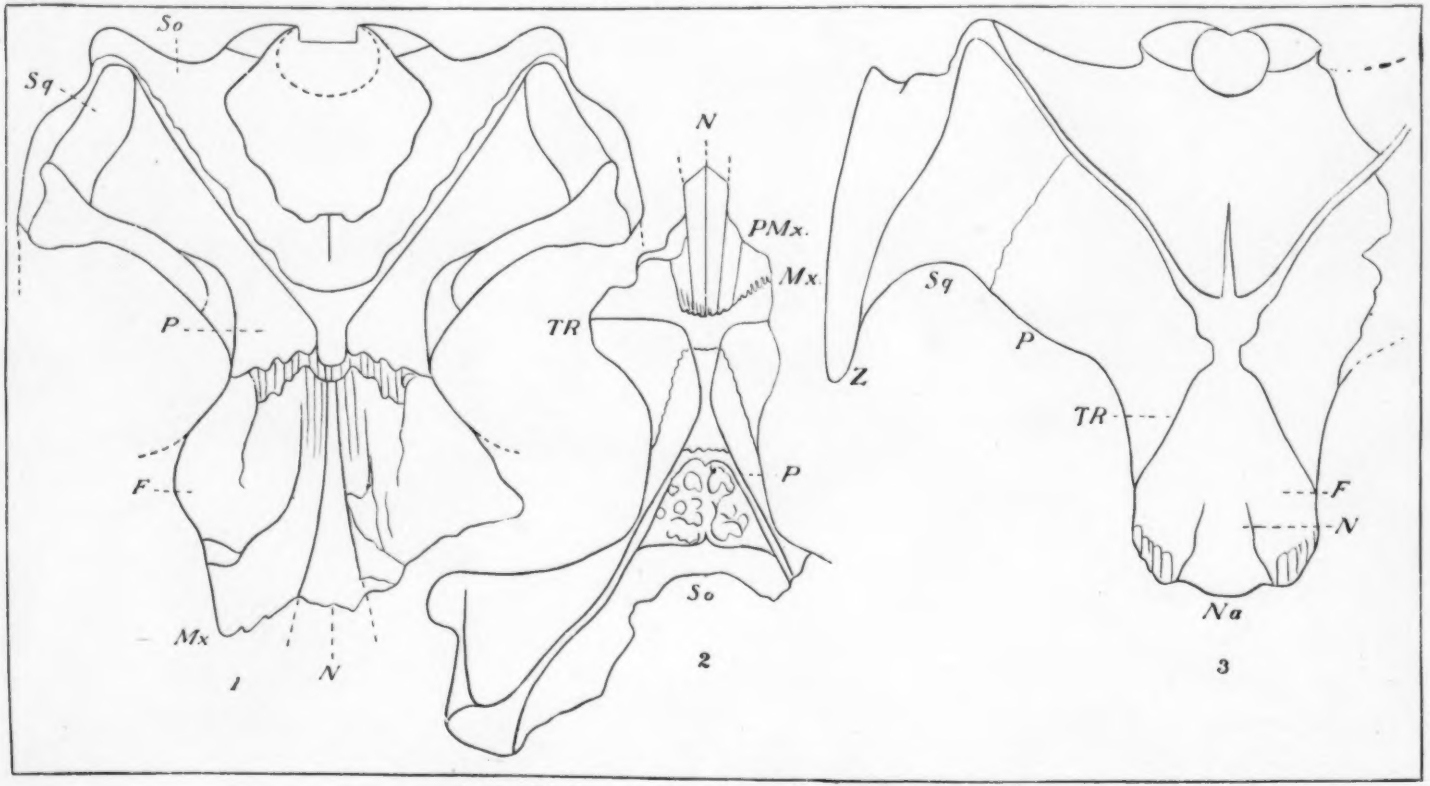
Fig. 5. *Rhegnopsis palæatlanticus* Leidy; Virginia.

Fig. 6. *Mesocetus siphunculus* Cope; Virginia.

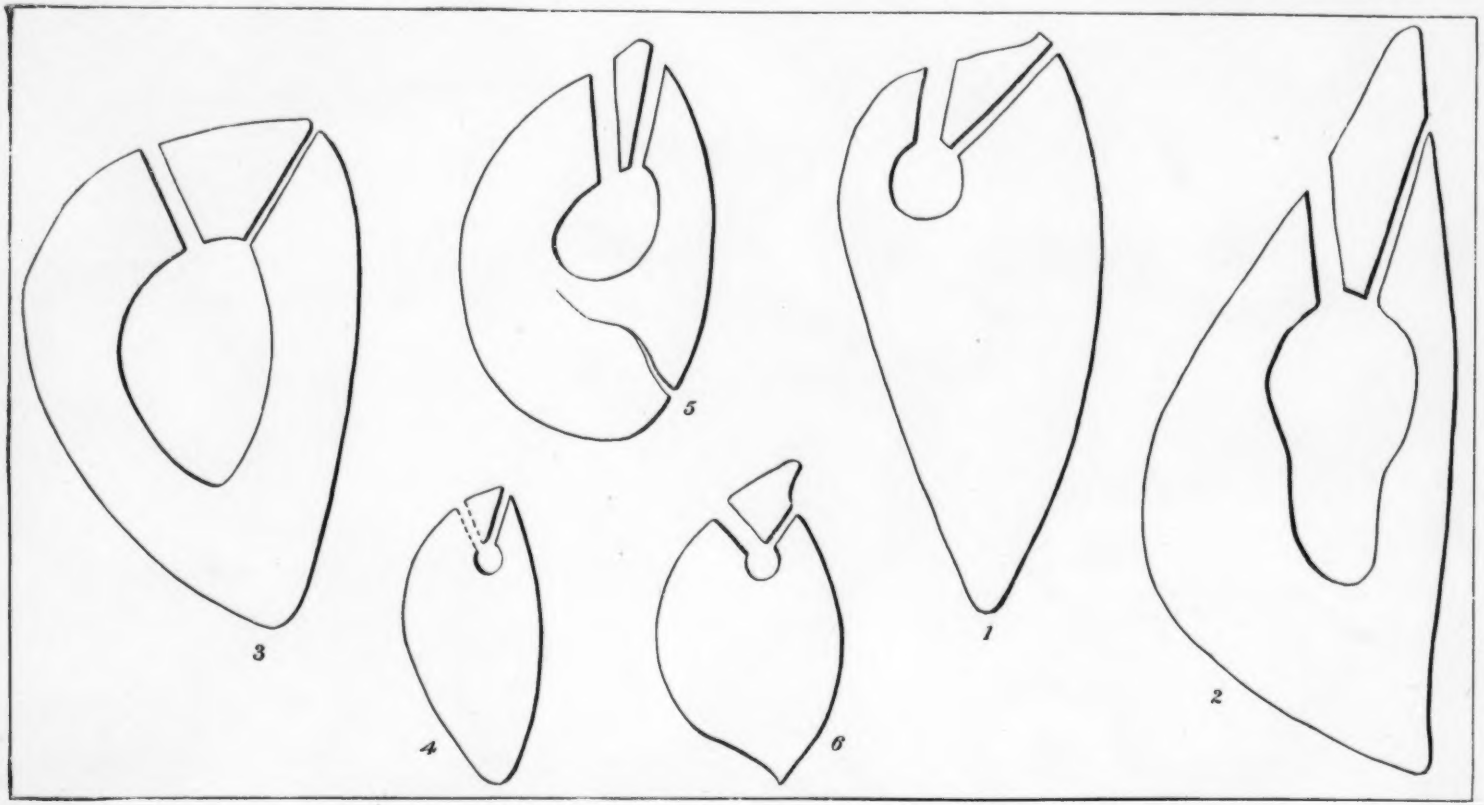
No. 1, Coll. Woman's College, Baltimore; 2, 3, 4, 5, Coll. Academy Natural Sciences, Philadelphia; 6, Coll. E. D. Cope.

Lettering.

So., Supraoccipital bone; *Sq.*, Squamosal; *Z.*, Zygomatic; *P.*, Parietal; *F.*, Frontal; *N.*, Nasal; *Na.*, External Nares; *Mx.*, Maxillary; *Pmx.*, Premaxillary; *T. R.*, Temporal Ridge.



1. *Cetotherium*. 2. *Cephalotropis*. 3. *Metopocetus*.



1–4. *Cetotherium*. 5. *Rhegnopsis*. 6. *Mesocetus*.

Notes on the Osteology of the White River Horses.

By Marcus S. Farr.

(*Read before the American Philosophical Society, May 15, 1896.*)

MESOHIPPUS.

Although nearly half a century has elapsed since *Mesohippus bairdi* was first described by Leidy,* our knowledge of its osteology has remained comparatively incomplete, all the known material being limited to foot bones and more or less complete skulls. Most all of the skeletons that were found were badly broken up and only the larger and more perfect bones were saved. Modern methods of collecting, essentially those introduced by Mr. J. B. Hatcher,† have revolutionized all this and now even the most delicate bones, though badly broken up, are preserved as easily as the large bones were before collecting was done in a scientific manner.

Fortunate discoveries of more complete skeletons during the last three years have given us very much better material and now enable us to supplement the accounts of *M. bairdi* that have already been given, to add many new points on the osteology of the species and to offer a restoration which is an improvement on those heretofore offered.

Several species of Mesohippus have already been made on material from Nebraska, Dakota and Colorado. These have either been founded on a few teeth presenting peculiarities or on foot bones not associated with teeth. These species have not been generally accepted, and the founding of species on such limited material especially in such a genus as Mesohippus which presents such a marked degree of individual variation does not seem justifiable and merely burdens science with useless synonyms. I have not seen the types upon which the various species, *M. exoletum*,‡ *M. agrestis*,§ *M. cuneatus*,‖ *M. celer*,¶ etc., have been established, but from the study of the individual variations in the many** specimens of *M. bairdi* studied by the writer it seems very evident that the species are not well grounded and that the peculiarities may be accounted for by the factor already mentioned.

The discovery of the Protoceras beds and their recognition as a distinct subdivision of the White River formations†† marks a stage in the development of the palæontology of this epoch.

* Leidy first described this species as *Palæotherium bairdi*, *Proc. Acad. Nat. Sci.*, 1850, p. 122.

† Curator of Vertebrate Palæontology in the College of New Jersey.

‡ Cope, *U. S. Geol. Survey of the Territories*, 1873.

§ Leidy, *Rept. U. S. Geol. Sur. Terrs.* (4to), i, p. 251, Pl. vii.

‖ Cope, *Palæontl. Bull.*, No. 16, p. 7, August 20, 1873.

¶ Marsh, *Am. Jour. Sci. and Arts*, 1874, p. 251.

** Remains of nearly one hundred individuals have been studied by the writer.

†† Wortman, *On the Divisions of the White River*, *Bull. Am. Mus. Nat. Hist.*, Vol. v, pp. 95–106.

The fauna of the Protoceras beds is unique in many ways, especially in the number of new and bizarre forms that come in, some evidently by migration, while others are the direct descendants of the species of the underlying Oreodon beds.

These strata are interesting, as they form a transition to the later John Day beds, their fauna being intermediate between the latter and that of the Oreodon beds.

A new species of horse has been found in this formation which helps very greatly in explaining the individual variations of *M. bairdi*, as many of these are seen to be attempts in the direction of *M. intermedius*, which is undoubtedly the direct descendant of the former. Besides these two species which are seen to stand in the direct relation of ancestor and descendant there is another species, *M. copei*, which occurs first in the strata of the Oreodon beds and is represented in the Protoceras beds by larger individuals.

Geological succession of the species:

Protoceras beds: *M. bairdi*, *M. copei*, *M. intermedius*.

Oreodon beds: *M. bairdi*, *M. copei*.

Titanotherium beds: *M. bairdi*.

The genus Mesohippus occurs then in all the different horizons of the White River beds. In the Titanotherium beds it is usually represented only by fragmentary remains, which, however, are unmistakably those of *M. bairdi*.

The Oreodon beds have yielded most of the best material. Through the whole extent of the fossiliferous strata of these beds, a vertical thickness of at least one hundred and eighty feet, remains of *M. bairdi* are fairly abundant. However, the remains are not well preserved, groups of teeth and the larger limb bones are common, while well-preserved portions of the skeleton are rare—a perfect skull has never yet been found. Beside *M. bairdi* we get in the upper Oreodon beds a new species which has been described as *M. copei*.* The Protoceras beds have yielded only fragmentary remains of *M. bairdi*. This species does not represent the main line of descent during this epoch, but it is here taken up by *M. intermedius* while the former still persists as a side line. We also get *M. copei*, which continues on from the Oreodon beds and is now represented by larger individuals.

Of *M. bairdi* nearly the entire skeleton is represented by material in the Princeton collection.

The skull has been quite fully described by Leidy,† and the skeleton has been the subject of an exhaustive paper by Prof. Scott,‡ but when this paper was written the entire skeleton had not yet been found and the incisor teeth of upper series are the result of explorations of the summers of 1894 and 1895, so some points in the description will be new.

*Osborn and Wortman, *Bull. Am. Mus.*, Vol. vii, pp. 356–358.

† *The Extinct Mammalian Fauna of Dakota and Nebraska*, Philadelphia, 1869.

‡ *Journ. of Morphology*, Vol. v, No. 3, December, 1891.

Moreover the description of this species *de novo* is justifiable because we wish to trace the steps in the evolution of the horse as they can be followed in the horizons of the White River strata and must therefore have a description of one species as a standard for comparison.

It is the purpose of this paper to add some new points on the osteology of *M. bairdi* and to give a new, more accurate and more complete restoration; to give a short description of *M. intermedius* and *M. copei*, and to show their relation to each other and to *M. bairdi*.

I must acknowledge my very great indebtedness to Prof. Scott, who has given me so much assistance in the way of suggestion and criticism and whose kindly interest in my work has ever been an inspiration during my three years of graduate study in Princeton. To Mr. J. B. Hatcher I am also very much indebted for free access to collections and for kindly criticism and help and for much information on White River mammals.

I must also extend my thanks to Prof. H. F. Osborn and Dr. J. L. Wortman, of the American Museum, for permission to study some of their very beautiful material; also to the latter for valuable suggestions.

The drawings are by Mr. R. Weber, and add materially to the value of the paper.

The Dentition

The dental formula is I. $\frac{3}{3}$, C. $\frac{1}{1}$, Pm. $\frac{4}{4}$, M. $\frac{3}{3}$. The dentition is thus seen to be unreduced, and the specialization or modernization consists in the complexity of the last three premolars which are molariform and Pm. 2 is beginning to assume the elongate character, so marked in the living horse by the elongation of the anterior part of the external half of the tooth. The characters of the permanent teeth have already been described by Leidy,* Osborn,† and Scott,‡ but very little has been written concerning the milk dentition and the superior incisors have only very recently been found. Only two skulls are known bearing the upper incisors, nearly all the skulls that are discovered having the end of the very narrow snout broken off.

The inferior canine is the smallest of all the teeth; it is suberect and conical, and there is a wide diastema between it and Pm. 1. The lower incisors are spatulate or chisel shaped and do not show any indication of a depression or pit. They have sharp cutting edges, and their inner surfaces are strongly concave. The first incisor is the longest (*i. e.*, highest above alveolar border) and also the widest of the incisor series. I. 2 is smaller than I. 1, while I. 3 is the smallest of the incisor series. There is thus a decrease in size and length of incisors outwardly towards the canine. The six incisors form an unbroken row.

* *Ancient Fauna of Nebraska*, pp. 70, 71; *Extinct Mam. Fauna of Dak. and Neb.*, pp. 305–309, 1869.

† *Bull. of Mus. of Comp. Zoöl.*, Vol. xvi, pp. 88, 89.

‡ "Osteology of Mesohippus and Leptomeryx," *Journ. of Morph.*, Vol. v, No. 3, pp. 303–305.

The anterior border of the mandible is rounded and the teeth are arranged in the segment of a circle.

The fourth lower premolar is wider transversely than any of the other teeth, while the posterior half of Pm. 3 is wider proportionately than any of the remaining teeth, with the exception of the former. Pm. 4 has a massiveness not seen in the other lower teeth. Sometimes this is so marked that if the teeth were not found together they would in all probability be attributed to a larger individual. It had long been supposed that the superior incisors were not pitted. Prof. Scott * has separated Mesohippus from Miohippus on the character of the upper incisors. A skull in the Princeton collection shows the upper incisors which seem to be pitted, but as they are so much worn a determination of their character is not possible. Osborn and Wortman † have just described these teeth and through the kindness of these gentlemen I have been permitted to examine this beautifully preserved skull. The two outer pairs of incisors show a distinct invagination, which is not, however, present on I. 1. Upper Pm. 1 is a small single-coned tooth, which has two distinct roots. The cingulum is well-developed on the inner side, enclosing a deep pocket. Anteriorly there is a tiny accessory conule. The corresponding tooth of the lower jaw is very small and inserted by only a single fang. Pm. 4 of the upper series is wider transversely than any of the other teeth.

Succession of the Teeth.

From all that can be observed the three large deciduous molars first appear simultaneously in both jaws. The next tooth to appear is that which represents Pm. 1 of the permanent set. Nothing is known as to the time of appearance of the incisors and canines, but judging from analogy we may presume that they appear as early as the milk molars. A mandible of Mesohippus (No. 11107), with milk dentition and M. 1 of the permanent set, shows alveoli for the three incisors and canine. The next tooth to appear (after persistent Pm. 1) is M. 1, which is succeeded by M. 2. Next the temporary molars are replaced by the permanent premolars.

In the upper jaw these are replaced in the following order: Pm. 4, Pm. 3, Pm. 2 (Pm. 1 persisting in both jaws). One specimen shows Pm. 4 almost ready to erupt, while Pm. 3 is very much smaller and the germ of Pm. 2 is very feebly developed. The mode of succession in the lower jaw seems to follow the same order. In specimen No. 10995, M. 1 and M. 2 have appeared, and the germs of the permanent teeth are seen by picking away the bone and exposing roots of teeth, where the germ of Pm. 4 is seen to be better developed than that of Pm. 3. This also accords with the rate

* *Trans. Amer. Phil. Soc.*, 1883, p. 79. In the light of present knowledge it seems best to abandon the genus Miohippus and to make the genus Mesohippus include the John Day equines as well as the White River forms.

† *Bull. Am. Mus. Nat. Hist.*, Vol. vii, p. 353.

of wear of teeth, as Pm. 4 is usually more worn by attrition than Pm. 3. After the deciduous teeth are replaced by those of the permanent set, M. 3 appears in both jaws.

It is not possible to tell from available material whether the incisors and canines are replaced or are persistent. In the later horse from the Equus beds, the incisors were certainly replaced, and the germ of canine is seen piercing the jaw. The foramen, through which it is growing, is large, but it is not possible to determine whether it had a predecessor or represents a permanent canine which does not appear until the other teeth are developed. Chauveau* makes the statement that the canine persists and is not replaced in the horse. However, judging from analogy, we are quite safe in presuming that in *M. bairdi* both the incisors and canines had predecessors in the milk series.

The Milk Dentition.

The temporary dentition may be given in the following formula:

I. $\frac{3}{3}$, C. $\frac{1}{1}$, D. $\frac{4}{4}$. See Fig. 1.

The tooth which represents Pm. 1 of the adult skull is not a true milk tooth, as it does not appear until the other teeth of the milk set are fully developed, and is not replaced as are the teeth of the temporary series. It may be considered a persistent milk tooth, as it has no predecessor, and then the dental formula will be as given above. If considered one of the permanent set, as there are ample reasons for doing, the molar formula will be: D.$\frac{3}{3}$.

Fig. 1.

Milk Molars of M. bairdi, $\frac{1}{1}$.
a, superior series.
b, inferior series.

The differences between the deciduous teeth and those of the permanent set are not due to any addition or reduction in the number of elements entering into the formation of the teeth, but are due to the difference in the relative development of the elements in the two sets. The differences can best be described by instituting a comparison between the two sets, and to do this it will be best to describe those of the permanent set and then show how the deciduous molars differ from them. The last two of the temporary set differ only in minute detail from the corresponding teeth of the later set, but there is a fundamental difference between Pm. 2 of the permanent set and its predecessor in the milk series.

All of the premolar teeth, with the single exception of Pm. 1, are molariform. Pm. 2 of both jaws presents some points of difference

* *Comparative Anatomy of the Domesticated Animals.*

from the other teeth, while the simple character of Pm. 1 has already been sufficiently commented upon. The last lower molar, as in so many forms, differs from the others in the presence of an additional less well-developed lobe situated posteriorly. The lower molars and Pms. 3 and 4 have oblong, quadrate crowns, with an outer pair of fore and aft principal lobes, and an inner pair of secondary lobes connate with them. "The principal lobes of the crown are slightly oblique in their relative position, angularly convex and sloping externally, concavely excavated internally and are acutely crescentoid at their summit. Of the inner secondary lobes, the anterior is much the larger, and is pyramidal in form with a twin pointed summit." This character is observable only in teeth that are not worn excessively and disappears as the summits of the crown are worn off in mastication. "The antero-internal cusp springs from the crown at the conjunction of the principal lobes and is continuous with their contiguous crowns. The posterior of the secondary lobes is conical and springs from the crown in conjunction with the back horn of the posterior principal lobe. The front horn of the anterior principal lobe curves inward, downward and backward to the base internally of the anterior secondary lobe. A basal ridge (or cingulum) nearly continuous bounds the crowns of the lower molars externally. Posteriorly it rises inward and terminates in a tubercle springing from the conjunction of the two posterior lobes." Pm. 2 deserves a slight mention in passing. In the lower jaw the posterior half of this tooth is an exact copy of the corresponding part of any of the succeeding premolars or molars. One half of the antero-internal lobe is present as usual, but this alone forms all of what corresponds to this lobe in the succeeding teeth. Anterior to this and externally there is another lobe more nearly median in position. This is connected with the former by a ridge and the two together form a lobe which is very different from any of the others. Anterior to this and connate with it is a small lobe on the internal surface of the tooth. The deciduous tooth differs from the permanent one in that in the former the two anterior lobes are more distinct from each other and from the other lobes, so that we seem to have five lobes in this tooth. Again in the earlier set this tooth has a greater antero-posterior extent than any of the other teeth, almost equaling in length M. 3 of the permanent set, which has the additional lobe. In the permanent set Pm. 2 is even shorter antero-posteriorly than the succeeding tooth in the premolar series. In the milk set D. 4 has the posterior half narrower than the anterior half. In D. 3 both halves of tooth are of approximately the same width, while, in the permanent premolar series the posterior half of the tooth is always the wider, while in the molar series the reverse condition obtains. The cingulum is not so well developed on the deciduous molars as on the corresponding teeth of the permanent set. It is not developed on the external surface of the posterior lobe as in the permanent tooth, but is present on the posterior border of tooth where it ends in a tubercle. The cingulum

is well developed on the antero-external lobe of Ds. 3 and 4, even better than on the corresponding permanent tooth. It has lately been called to my attention that the cingulum varies in the individual with the nourishment, well-nourished individuals having it better developed than those poorly nourished, but the recurrence in many individuals of the character as given above precludes the possibility of its being an individual variation. The antero-internal cusp is wider antero-posteriorly in the temporary teeth than in the permanent set and the bifid character of this cusp is more marked in the former. All the lower milk teeth are narrower and longer antero-posteriorly than the permanent teeth. Both the upper and lower molars of the deciduous set are of not nearly so great vertical length as those of the later series.

The Upper Molars.

Premolars 2, 3 and 4 are molariform and Pm. 2 is beginning to assume the elongate character which is so much emphasized in the living horse. The six molars (*i. e.*, molars and molariform premolars) are nearly alike in size and form. "They have square crowns, wider transversely than broad antero-posteriorly and both these measurements greatly exceed the length. The crowns consist of three pairs of lobes—an outer and an inner pair of principal lobes and a much smaller pair situated between them, the secondary or accessory lobes. The outer lobes are demi-conoidal and form at their junction a narrow buttress externally. A stronger buttress bounds the fore part of the anterior of the two lobes. A tendency to the development of a buttress is seen also at the back part of the posterior of these lobes. The buttresses expand and are conjoined at the bottom of the crown, forming together a pair of arches bounding the external surfaces of the outer lobes. These surfaces are nearly flat and are divided by a conspicuous median ridge. The inner surfaces of the outer lobes are prominently or almost angularly convex. The inner lobes of the crown are simply conical, wider transversely than fore and aft and with the anterior slightly larger than the posterior. The median lobes are not more than half the size of the principal ones and appear as prominent folds curving outwardly from the inner lobes to the anterior face of the outer lobes. Elements of a basal ridge exist at the fore and aft parts of the crown and at the outlet of the valley separating the inner lobes. In the interval posteriorly between the back inner and outer lobes there exists a tubercle which in association with the contiguous portions of the basal ridge assumes the dignity of a sublobe." In Pm. 1 the anterior buttress is more distinct or separate than in the other molars, though it is not so large. The anterior of the median cusps is larger than the posterior, except in Pm. 2, which is peculiar in this as in so many other respects.

The teeth of the temporary set present the following differences from those of the permanent set described above:

1. The cusp situated between the outer and inner posterior lobes, the

so-called hypostyle, is less well developed in the deciduous molars than in those of the permanent set.

2. D. 2 is much larger, more elongate antero-posteriorly, more complex, the antero-external buttress being much larger and more distinct in the earlier set. It is so large that it might almost be considered a fifth principal lobe.

3. The median accessory lobes (5 and 6) are more conical than in the permanent set, where they are somewhat appressed. These lobes in the early set are separated by a distinct notch from the internal lobes.

4. The transverse ridges are more nearly confluent with the outer wall of tooth in most of specimens in the temporary set. There is, however, great individual variation in regard to this character.

5. In the adult skull all the molars and molariform premolars are much wider transversely than antero-posteriorly. The deciduous teeth are more nearly square, the two diameters being subequal.

6. The buttress on the antero-external lobe of tooth, the parastyle, is better developed in the milk set.

7. D. 2 is the longest tooth of the milk series and is beginning to assume the elongate character of this tooth in the modern horse, while the corresponding tooth of the permanent set is smaller than any of the other molar teeth.

8. All the temporary teeth are shorter in vertical height than those of the permanent set.

The Vertebral Column.

The cervical and dorsal vertebræ have already been minutely described. The lumbar vertebræ are almost certainly five in number. The centra are large and are reniform in shape, being wide transversely and not having the more nearly circular outline of the median dorsal vertebræ. All of the lumbars, with the exception of the last, have their centra strongly keeled. The centra are moderately opisthocœlous. The interlocking character of the vertebræ through the zygapophyses is marked. The neural spines are long, transversely compressed and narrow and have considerable antero-posterior extent. They are all directed forward at an angle. The transverse processes are well developed and widely expanded. The intervertebral foramina perforate the bases of the neural arches, and are not merely notches in the ends of the neural arch as they are in the anterior vertebræ of the column. The last two lumbar vertebræ have their transverse processes expanded almost as widely as those of the first sacral itself, and the transverse processes of the fourth lumbar abut against those of the fifth, while the latter bears on the posterior surface of the transverse processes deep concavities for the corresponding surfaces of the anterior end of sacrum. An analogous condition is seen in Equus, and in old individuals the last two lumbars are very frequently immovably coössified. The last lumbar has the spine more nearly erect than that of the penultimate lumbar vertebra.

A very remarkable character of the lumbar vertebræ is that they have spines which are nearly, if not quite, as high as those of the anterior dorsal region, which in the horse are so much elongated. In the latter the lumbars have spines which are lower, more nearly erect, of more considerable antero-posterior extent proportionately and are much less compressed transversely.

The Sacrum.

The sacrum of *M. bairdi*, as in most of the Ungulata, consists of one broad vertebra joining the ilia, followed by a series of narrower ones, gradually diminishing in width anchylosed to it behind. These latter diminish in width very gradually. In living Ungulates the number of vertebræ entering into the formation of the sacrum varies with the age of the individual and also varies in individuals of the same age.

Fig. 2.

Sacrum of M. bairdi, ⅔. Inferior view.

In the specimen which belongs with the pelvis described below there are six vertebræ. This is the most perfect sacrum of *M. bairdi* yet found, and the component vertebræ are fortunately well preserved and hardly crushed at all (see Fig. 2 and Plate xiii).

The first or true sacral vertebra is greatly expanded transversely and bears large articular surfaces for the ilia.

Anteriorly there are large convex facets which fit into the corresponding concavities in the transverse processes of the last lumbar vertebra. The first sacral has a low and comparatively wide centrum. The spine is very high, very much compressed laterally, as are all the spinous processes of the vertebræ, and is directed strongly forward, while in the modern horse it is almost vertical. The five succeeding vertebræ have transverse processes which are not so widely expanded, the centra are very much depressed and the neural arches are low and gradually decrease in height posteriorly. This, of course, conditions the size of the neural canal, which in this region is very much attenuated. The expanded transverse processes of the contiguous vertebræ are all united, so that they form a narrow elongate plate. The spine of the second sacral is gone, but the others are all preserved. That of the third is almost vertical, while the spines of the three posterior sacrals all slope backward at a decided angle. There is thus a very abrupt transition in the direction of the inclination of the spines from the first in which the spine projects forward to three in which the process is almost vertical. The plate formed by the anchylosis of the centra and transverse processes of the vertebræ is concave inferiorly or curves downward posterior to first sacral. The sacrum presents inferiorly the foramina for the five pairs of sacral

nerves, the inferior sacral foramina, while above we also find laterally between the neural arches of the contiguous vertebræ the five pairs of the superior sacral foramina.

Measurements of the Sacrum.	MM.
Length	116
Extreme width	64
Width third sacral	23
Width fourth do.	21.5
Width fifth do.	20

The Caudals.

The few caudal vertebræ preserved are sufficient to give us a general idea of the character of the tail. The first caudal has very widely expanded transverse processes similar to those of the posterior sacral region; the centrum is oval and the neural arches arise at a very great angle enclosing a high and very narrow neural canal. The transverse processes are of considerable antero-posterior extent, but do not equal the length of the centrum in width as they do in the posterior vertebræ of the sacral region. It is not possible to determine how many of the caudal vertebræ had complete arches, because of incomplete material. In Equus* the spine of the neural arch is bifid in the second caudal and the arches are incomplete on the third. The transverse processes gradually become shorter, the neural arches more rudimentary and are finally lost, and all we have is a cylinder of bone with very rudimentary processes which gradually diminish in size. Among the caudals preserved is one of these last, in which all the processes are very feebly developed. All the vertebræ of the tail are in general like those of the horse, and in them, as in most all of the anatomical features, we see a foreshadowing of what the future horse is going to be.

The Sternum.

With the almost complete skeleton figured in the restoration of *M. bairdi* in Plate xlii are preserved three segments of the sternum. These are the xiphisternum and two segments of the mesosternum. The former is very much more elongate and not so high as the other divisions of the sternum. Anteriorly it is about twice as broad as high, while posteriorly it is very much flattened. The free border is thin and rounded with irregular surface, showing where cartilage was attached. Laterally the body of this segment as of all the other is concave. The superior border is almost plane, while the inferior is slightly concave, or the free end may be said to project slightly downward.

The next segment in front of the above that is preserved is very evidently the penultimate segment of the mesosternum. This is very different in shape from the xiphisternum. The posterior portion is wide and

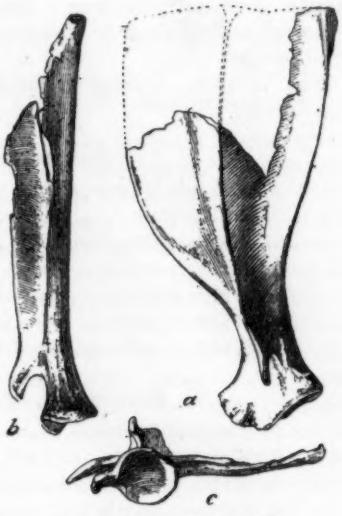
* No. 338, Princeton Coll.

low, while anteriorly it is much narrower and higher. Both superior and inferior surfaces are plane and the sides are very strongly concave. The third segment is evidently the first division of the mesosternum, and is high and long and almost trihedral in cross-section. These separate segments of the sternum are not coössified, and the surfaces for the articulation of the sternal cartilages of ribs are not well shown. From the portions of sternum described above we are safe in assuming that there were at least six segments in the sternum of *M. bairdi*.

The Scapula.

The nearly complete skeleton from which the restoration given herewith is made fortunately has the scapula very well preserved, and this reveals quite an unexpected character, viz., the presence of a distinct acromion. The only other Perissodactyl known to have retained this process is Pachynolophus (Orohippus) of the Bridger Eocene. Marsh * has described it in this genus as follows: "The scapula has a prominent acromial process, which is compressed and decurved as in some Carnivora." Mesohippus is the only Perissodactyl known to have retained this process until Oligocene times, and it has thus been retained longer by the horses than by any other family of this order. It is possible that future discoveries may also reveal the presence of a clavicle in Mesohippus, as it has been discovered in the contemporary *Oreodon culbertsoni*,† and in the latter genus it persists until Deep River times, where it has been found by Prof. Scott ‡ in the form which he has called Mesoreodon. The possession by both Mesohippus and Pachynolophus of this process would seem to justify us in regarding the latter as the Bridger ancestor of the horse line of which Mesohippus is the White River representative. The scapula is wider in proportion to its height than that of Equus. The anterior margin is very thin and strongly

Fig. 3.



Scapula of M. bairdi, 3/8.
a, from outside.
b, from behind.
c, from below.

* *Amer. Jour. Sc. and Arts*, Series 3, Vol vii, 1874, p. 247

† A specimen in the museum of the University of Chicago reveals the presence of the clavicle.

‡ *Trans. Amer. Philos. Soc.*, Vol. xvii, p. 136.

convex, while the posterior border is only slightly rounded and is very much thickened, a character that has been retained by the Equidæ, Tylopoda, Pecora and Suina, but has been lost in the Tapiridæ and Rhinocerotidæ. The spine of the scapula is very high and seems to extend nearly or quite to the vertebral border. It is much nearer to the anterior border than the posterior, thus making the prescapular fossa much smaller than the postscapular.

The spine becomes gradually more prominent towards the middle portion, at which point it seems to have been highest and the edge was here strongly retroverted as in Tapirus and Rhinoceros. From this point it decreases in height towards the vertebral border.

The acromion is styliform in shape, is compressed antero-posteriorly and extends outward and downward, but does not quite reach the level of the glenoid cavity. It resembles in shape that of the camel and llama, but differs from these in that they are more slender, more nearly perpendicular and extend nearly or quite to the level of the glenoid cavity. The process gradually tapers towards the free end, which is somewhat rounded. The neck of the scapula is very much constricted and is comparatively long. The glenoid cavity is quite deeply excavated, is very slightly elongate antero-posteriorly and has a well-defined rim.

The coracoid process is strong, curves inwardly and is slightly retroverted.

Measurements of Scapula.	MM.
1. Extreme length	136
2. Width of neck	18
3. Width of distal end	32
4. Extreme width	74
5. Width at highest point of spine	74
6. Width of supra-spinous fossa here	25
7. Width of infra-spinous fossa here	45

*Measurements of Scapula of Equus.**	MM.
1. Extreme length	414
2. Width of neck	73
3. Width of distal end	107
4. Extreme width	186
5. Width at highest point of spine	146
6. Width of supra-spinous fossa here	48
7. Width of infra-spinous fossa here	93

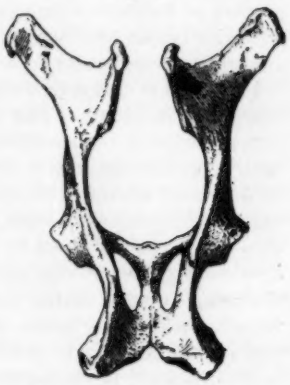
These measurements show the scapula of *M. bairdi* to have been proportionately more expanded superiorly than that of the horse and at the same time the neck is proportionately more contracted than in the latter.

*No. 338, Princeton Coll.

The Pelvis (No. 11376).

The pelvis is equine in all its characters and very much like that of the modern horse with some characteristic points of difference. The specimen described below is the first pelvis of *Mesohippus bairdi* that has ever been found showing all the characters, being almost perfect. See Fig. 4, and Plate xiii. It was discovered by Mr. J. W. Gidley during the past summer in the lower Oreodon beds.

Fig. 4.



Pelvis of M. bairdi, ¼.

The most striking difference between the pelvis of *M. bairdi* and that of the horse is that the former is narrower in proportion to its length than that of Equus.

The great breadth of the pelvis anteriorly in the latter is owing to the very great lateral expansion of the ilia, while in the earlier genus they are proportionately less widely expanded. The ilia directly in front of the acetabulum are slender in their proportions and expand more gradually than in the horse, so that they are longer in proportion to their width than in the latter. The bone is widely expanded superiorly and the angle above the point of articulation of the ilium with the sacrum curves upward and outward, and the free end is thickened and somewhat rugose. This upward and outward expansion of angle makes the external border of superior aspect of the ilium concave. The crest is more slender and elongate comparatively than in Equus and is strongly everted. The border of the ilium between the angle and the crest is very thin and strongly concave. The whole anterior expanded portion is thin except along the outer or lower border. The posterior border of the angle above the point of articulation of the sacrum is also slightly thickened. The sacral border of the ilium is large and extends high above the articular facet for the sacral vertebræ forming the angle. The ilia as well as the long axis of pelvis are directed downward at an angle from the vertebral column. The acetabulum is an elongate oval in shape and its borders are elevated and well-defined. The border is incomplete below owing to the encroachment of the pit for the ligamentum teres on the acetabular fossa. This is less emphasized, however, than in the horse. The pit for the ligamentum teres is quite deep.

The ischium is straight and on a line with the long axis of the ilium. The bone curves outwardly posteriorly, but does not curve upward as in the horse. The posterior border is expanded and thickened outwardly where it ends in a stout process, the tuberosity of the ischium. The internal border posteriorly is deflected towards the median line and meets

its fellow of the opposite side at this point forming part of the symphysis. Above the acetabulum the border of bone is high and rounded, but is not sharp and angular as in the horse. The obturator foramen in the pelvis of the latter is rounded and shorter in proportion to its width than in *M. bairdi*, being only slightly elongate, while in the species under consideration the foramen is narrow and very much elongated, the length equaling twice the breadth. This conditions the shape of the posterior portion of ischium, which in *M. bairdi* does not extend far back of the posterior border of obturator foramen, while in Equus the ischium forms a large expanded plate posterior to the obturator foramen.

The pubis is elongate, flattened from above downward and irregularly triangular in shape. The portion of pubis nearest the acetabulum is almost round in cross-section, while in the horse the corresponding portion, as in fact the entire pubis, is very much more flattened. It meets its fellow of the opposite side in the median line forming the anterior part of the symphysis with the bases of the triangles applied together The symphysis is formed by both pubes and ischia conjointly, the former constituting the anterior and larger part while the ischia form the posterior part. Fusion of the pubes is so complete that no trace of a suture remains, while the ischia are not anchylosed together. The anterior part of the symphysis is flattened in the form of a large plate, which bears inferiorly in the median line a prominent spine. All the processes for muscular attachments are less strong and rugose than in the horse. The pelvic foramen (or cavity) is longer in proportion to the breadth in *M. bairdi* than in the horse, being a little longer than broad, while in the latter the pelvic outlet is broader than long. In Mesohippus the length (or vertical height) is about 65 mm. and the breadth 60 mm., while in the horse the reverse condition obtains and we find a length of only 174 mm. as compared with a width of 199 mm.*

Other measurements of the pelvis are as follows:

	MM.
1. Extreme length	209
2. Length of acetabular cavity	26
3. Length of symphysis	63
4. Extreme width of ischia	74
5. Width at acetabulum	102
6. From top of angle to outer point of crest	89
7. From anterior border of acetabulum to point midway between angle and crest	74

Restoration of M. bairdi (Pl. xiii).

In 1879, Prof. Marsh,† in giving the genealogy of the horse, brought out the fact that the chief modifications through which the horse passes in its evolution are the following:

1. Progressive increase in the length of teeth and in their complexity,

* ($6\frac{7}{10}$ x $7\frac{7}{10}$ inches) Chauveau *loc. cit.*

† *Am. Jour. Sci.*, Vol. xvii, p. 497.

from a very short-crowned tooth with distinct roots, to one with very long crown in which roots are not formed till animal becomes adult.

2. The gradual lengthening of the limb bones with the suppression of the lateral digits and the concentration of the growth force in metapodial iii, producing ultimately a monodactyl foot from a pentadactyl ancestor.

3. The continued reduction of ulna and fibula and their ultimate coalescence with the radius and tibia.

4. Gradual increase in size from an animal not larger than a fox up to the modern horse.

Mesohippus bairdi is an interesting intermediate stage in the evolution of the horse; though primitive in many respects, it had already made considerable advance over its Uinta predecessor.

The restoration here given is made from a nearly perfect skeleton which enables us to make some improvements on the one already given,* which, however, was as good as could be made with the material then available.

The lumbar vertebræ, sacrum, pelvis and a few of the posterior dorsals are from another individual reduced to proportion. Part of the skull is also restored from another specimen.

Mesohippus occupies a position about midway in the line of descent of the horse series. It presents the following advances over its Bridger predecessor, Pachynolophus.

1. The teeth are longer (vertically) and more complex, the intermediate cusps are better developed, and the transverse ridges are likewise better developed and more nearly confluent with outer wall of tooth.

2. The lateral metapodials are more reduced comparatively, and metapodial iii is much larger. In the Bridger form the phalanges of the fifth digit are present, but *M. bairdi* has lost these.

3. Both the ulna and fibula are more reduced than in the earlier form

4. In *M. bairdi*, Pms. 2–4 are molariform, while in Pachynolophus Pm. 4 only is molariform and is smaller than true molars. Epihippus, the Uinta representative of the series, has Pms. 3 and 4 molariform, and this is the only generic distinction between the Bridger and Uinta genera.

The orbit is commencing to retreat, though it is still over the molars, the anterior border being directly over the posterior half of M. 1. In the horse it is situated posterior to molar series, and we can trace a gradual transition in the position of orbit up through the different genera from Mesohippus to Equus. This shifting backward of the orbit brings about a gradual elongation of the facial region of the skull. The alveolar border of the maxillaries is low, this of course being associated with low-crowned, short-rooted teeth.

From the character of the teeth we may judge of the life habits of the animal. The teeth of the modern horse have very long crowns

* *Journ. of Morph.*, Vol. v, No. 3, p. 337.

(hypsodont), grow from persistent pulps and do not form distinct roots until the animal is quite old, not until a length of crown is attained which under normal conditions will afford sufficient grinding surface for an average lifetime. As the teeth wear off by attrition the loss is replaced by growth, and growth and wear proceed pari-passu until the animal becomes adult.

The little Mesohippus, with its short-crowned (brachyodont) teeth, inserted by distinct roots, must therefore have fed on succulent plants that grew in swampy, marshy land—as if subjected to wear necessitated by the mastication of the hard, silicious grasses of Miocene times, the teeth would soon have worn out entirely and the animal would have succumbed to starvation. In most of the specimens found the teeth are only moderately abraided.

The feet, too, being tridactyl are adapted to progression along the oozy shore of rivers or to swampy, marshy ground as the toes would spread and thus support the animal in the mud, while the monodactyl foot of the horse is preëminently adapted for rapid locomotion over the grassy plains. This would seem to prove that the life habits of the animal have changed very greatly during its evolution. Many of the White River animals were adapted by their anatomical structure to life in swamps. Some were at least semi-aquatic in their habits, as is denoted by the position of the posterior nares, which in some forms are removed very far backward, *e. g.*, Ancodus.

The skull is equine in its characters, but is still quite small and the facial region is short. The orbit is not enclosed behind.

The neck is long, and, as in the horse, these vertebræ are larger than those of the dorsal region of the column. The processes are not so massive as in Equus, but are quite as complex and are very well developed. The spines of the dorsal vertebræ are not so high as we should expect, and very evidently *M. bairdi* did not have any great elevation of the anterior dorsal region. The modern horse is much higher at the withers than at the haunches. The spines of the lumbar vertebræ are very high and incline forward at quite an angle. There is a very abrupt transition in height of spines from the first sacral, which has a very high spine to third sacral, which has a very much lower spine, though it is still much compressed laterally. Six vertebræ take part in the formation of the sacrum. The centra of the first few caudals are flat with wide transverse processes, but these, as well as all the other processes, gradually become suppressed and the neural arches disappear so that the lower caudals are merely cylinders of bone. It is impossible to determine the exact number of vertebræ taking part in the formation of the tail, but it is fair to imagine that it had one at least as long pro portionately as the horse.

The scapula is remarkable for the persistence of the acromion process, in which character it is unique among all Perissodactyls, with the exception of Pachynolophus (Orohippus) of the Bridger. The spine is better

developed, the bone is lower and broader, the neck is more constricted proportionately than in the horse. In the latter the anterior border of the scapula is not rounded as in Mesohippus. The ulna is very much reduced in *M. bairdi*, and the radius is enlarged to sustain the weight of body. The ulna is distinct from the radius through the whole of its extent, the two bones not being coössified even in old individuals. Below the proximal half the bone is much compressed and tapers rapidly toward the distal end. This gives it a frail character so that it is almost always broken away in fossilization, and only recently have specimens been found which permit an accurate determination of its character. The distal end is not compressed as it is higher up, but is round in cross-section and bears a facet for the cuneiform. A rudiment of the fifth metacarpal persists. All the metacarpals and their phalanges are somewhat shorter and less massive than the metatarsals and the phalanges of the hind foot. The pelvis is thoroughly equine and yet differs in many minor characters from that of the horse. It is narrower in proportion to its length than that of the latter. The ilia expand less abruptly, the crest is narrower and more elongate proportionately, and the ischia do not bend upward posteriorly as in the horse, but are in a straight line with the long axis of the ilia. The obturator foramen is more elongate and narrower transversely, and the pelvic outlet is higher and narrower proportionately than in the modern equine.

The fibula was complete in *M. bairdi;* was very much reduced in size and was coössified with the tibia. The proximal end is quite small, the shaft is filiform, while the distal end alone is quite large and forms the external malleolus articulating with the astragalus, and in extreme extension of the foot also with the calcaneum. The fibula remains complete until John Day times, for in *Mesohippus* (*Anchitherium*) *præstans* Cope from this formation it is retained in its entirety.

The hind limbs are much longer than the fore limbs, more so proportionately than in the horse, so that the rump must have been much elevated above the withers if the different elements of the limb were not very much more flexed on each other than would seem justifiable, judging from recent animals. Many of the White River animals had a curved arched back instead of a straight back as in the horse, *e. g.*, Hyænodon, Leptomeryx, etc. This is shown by the character of the centra of the vertebræ. The great individual variations met with in *M. bairdi* have been noticed by every investigator who has studied a series of specimens of this species. These variations are principally in the limbs and teeth. Some of these have already been noted. In several individuals the three cuneiforms of tarsus are all coössified into a single compound cuneiform. Usually the ento- and meso-cuneiforms are united.

There is usually a moderately large contact of metatarsal iii with the cuboid, this latter usually extending below the level of the ecto-cuneiform, so that all contact of metatarsal iii with cuboid is lateral. In some specimens there is a slight extension outwardly of the proximal

end of M. iii and the cuboid is slightly shorter, so that it articulates with the distal end of cuboid instead of being confined to mere lateral contact. The antero-internal angle of cuboid is accordingly somewhat modified in shape to correspond with the changed outline of metapodial iii. This is a tendency in the direction of *M. intermedius* of the Protoceras beds, and a foreshadowing of the condition in the modern horse which has such a large facet on the cuboid for the widely expanded proximal end of metatarsal iii. Between this condition and that where there is only lateral contact with the cuboid, we find all the intermediate stages. Again, there is a great deal of variation in the relative proportions of the lateral digits to each other, and in the relation they bear to the median digit. Sometimes the lateral digits are not much reduced and are subequal in size, while again we find the lateral digits very much reduced, and Mt. iv, at least proximally, is usually larger than Mt. ii.

In *M. bairdi* usually there is no confluence of posterior transverse crest with the outer wall of tooth, usually separated from it by a large interval, but occasionally we get an individual in which there is actual confluence, and we get all stages intermediate between these two extremes. We get individuals where the interval between outer end of transverse crest and outer wall is less, and, again, others in which there is a small process jutting inward from the point of union of outer lobes, toward the transverse crest, these separated by a very small interval, and then we get complete confluence. These highly specialized forms were, of course, not ancestral, but were prematurely modernized and left no descendants. However, these individuals most specialized occur highest up in the beds, showing that these variations are attempts in the way of evolution.

Mesohippus Copei.

This is a new species of horse from the White River, which has just been described by Osborn and Wortman.* In their description of the type no specific characters other than those of size are given, by which it may be distinguished from the two other species from this horizon. This species was founded upon a complete half of a pelvis, femur, tibia and part of a hind foot, together with a median metatarsal and one lateral metatarsal of another individual, a collateral type. "These remains indicate an animal of much larger size than those of *M. intermedius*, and, so far as we know, is the largest horse of the White River epoch, even larger than *Mesohippus* (*Anchitherium*) *præstans* of the John Day." The species is undoubtedly well founded, but the material in the Am. Museum did not permit the establishment of good specific characters. I have studied carefully the material upon which the species is founded and have been able to refer some material in the Princeton Collection to this species. This material consists of the distal end of a

* *Bull Am. Mus.*, Vol. vii, pp. 352-358.

femur, tibia and almost complete hind foot, and enables me to give some further characters of the species. *M. copei* differs from *M. bairdi* in the following respects: (1) The lateral metapodials curve outwardly quite sharply distally and the toes were thus more spreading than in *M. bairdi* (see Fig. 5). (2) The meso-cuneiform is proportionately less deep than the ecto-cuneiform than in *M. bairdi*. (3) The carina or median keel of the distal end of metatarsal iii, which in the smaller species is almost entirely confined to the plantar surface of the bone, in *M. copei* extends far up in the dorsal surface of the distal end of the bone. (4) The lateral metapodials are comparatively shorter than the median metapodial, so much so that the ungual phalanges could scarcely have been functional at all, and this form had progressed farther toward monodactylism than any other known form from the White River. (5) The combined depth of the navicular and ecto-cuneiform was greater than in *M. bairdi*, and greatly exceeded that of *M. intermedius*. (6) The cuboid did not extend below the level of the ecto-cuneiform. Metatarsal iii was borne by the latter alone and did not extend over on the cuboid, so that anteriorly there is no contact of these two bones either lateral or distal as in both the other species.

The tibia is about one and one-half times as long as that of *M. bairdi*, and is proportionately much stouter.

The shaft is very long, even longer than that of the John Day species, but is more slender, and seen from the side it presents the characteristic sigmoid curve. The cnemial crest is very high, curves slightly outward and has the usual tendinal sulcus on its outer border. It extends farther down on the shaft than in *M. bairdi*. The proximal surface is very much more rugose than in the latter. The femoral facets slope downward and backward at quite an angle. The outer facet is convex antero-posteriorly and concave transversely. The inner facet is concave antero-posteriorly and convex transversely. The distal end of tibia is turned slightly outward. The distal end of tibia and fibula together are proportionately wider than those of *M. bairdi*. The facets for the trochlear surface of astragalus are deeply incised, are oblique in position and are separated by a high intertrochlear ridge.

The proximal end of the fibula is not preserved, but the very large distal end and a portion of the shaft persists. Rugosities on the outer border of tibia indicate that it was complete and closely applied to the latter. The portion of the shaft preserved is very much reduced. The expanded distal end forms the external malleolus and bears the two usual facets.

The tarsus presents striking differences from that of *M. bairdi*, and can best be described by instituting a comparison between it and the latter.

The calcaneum is stouter and more massive, but has about the same relative proportions as in *M. bairdi*. The tuber calcis is large and rugose for the insertion of the tendo Achillis. The tuberosity is quite high

with its inferior border slightly convex. The upper border is broken away. The tuberosity is much thicker and more massive than in the smaller species, where all the bones are gracefully shaped. The sustentaculum is very strongly developed and bears a large facet for the astragalus, which facet is elongately oval in shape. The crest formed by the superior or ectal astragalar facet is broken off so that its character cannot be determined. There is a slight prolongation of this facet antero-externally which is somewhat more emphasized than in the smaller species. The inferior facet is near the distal end, and is the smallest of all the facets of calcaneum, and does not extend far back from the distal end—elongate in shape. The facet for the cuboid is large, occupying all the distal end of the bone which is more obliquely truncated than usual. The shape is triangular with the apex towards the sustentaculum.

Fig. 5.

Left Foot of M. Copei, ¼.

The astragalus is merely an enlarged copy of that of *M. bairdi* with some differences of detail. It is proportionately broader. The trochlea is more widely open and the condyles are higher and thicker. The neck is of about the same relative proportions as in *M. bairdi*. The internal condyle as usual is the longer of the two and anteriorly slightly overhangs the navicular facet while in the smaller species it does not quite reach it. The outer condyle is very much shorter than the inner and is separated from the navicular facet by quite an interval.

The navicular is a flat bone, is wide transversely and seems proportionately higher than in *M. bairdi*. The proximal articular surface is strongly concave antero-posteriorly for the corresponding surface of astragalus. Posteriorly there are two elevations on the inner and outer borders respectively, between which is a wide and shallow depression for the projection on the inferior margin of distal surface of the astragalus. The external margin of this latter projects strongly downward, extending around the outer edge of navicular. These two characters make a very close interlocking joint so that there is scarcely any direct lateral movement possible. This interlocking is not quite so complete, however, as in *M. bairdi*, as in this latter the external margin of inferior surface of astragalus extends farther down on outside border of navicular. This outside projecting border is in the form of a crest which is placed obliquely on bone and limits the direction of the movement of the two bones taking part in this articulation on each other to an oblique motion. The distal surface of bone presents a large triangular facet for ecto-cunei-

form. Coalescing with apex of above is a facet extending up on posterior border of bone, which articulates with cuboid. On the proximal surface there is a small facet on the antero-external corner of bone, which articulates with the calcaneum by a small facet just above the inferior astragalar facet and which seems to be a part of the latter, but on close examination proves to be a distinct facet. In *M. bairdi* the navicular just touches the calcaneum, but does not have such distinctly marked facets. This character is seen in some individuals, but in all observed specimens the contact is smaller.

The ecto-cuneiform is high and massive, the breadth being twice the height. The proximal facet for navicular is concave, both antero-posteriorly and transversely. The inferior (or distal) facet is concave in both these directions. On the external side it abuts against the cuboid, and this latter seems to have been just equal in length to the combined length of ecto-cuneiform and navicular. It bears no facet either lateral or proximal for metatarsal iv.

The coössified ento- and meso-cuneiforms show an emphasized condition of that of *M. bairdi*, in that the tendency of the distal row of tarsal bones to form a closed circle is more marked here. The portion representing meso-cuneiform bears most all of the proximal end of metatarsal ii. The ento-cuneiform is high and compressed transversely and curves strongly backward and around towards the other side of foot. On its inferior surface it bears a facet at its point of contact with metatarsal ii.

The metatarsus of *M. bairdi* exhibits the following characters: (1) The cuboid which bears metatarsal iv extends down below the external cuneiform which bears M. iii. (2) The meso-cuneiform does not quite reach to level of the ecto-cuneiform. From this it results that M. iv does not quite reach up to level of M. iii, while M. ii reaches above the latter. In *M. copei*, M. iv extends quite up to the level of M. iii, while the meso-cuneiform is not so deep proportionately as in the smaller species. Metatarsal iv is proximally much less reduced than M. ii, but tapers to about the same size distally. It is borne entirely by cuboid. The disproportion in size of the proximal ends of the two lateral metapodials can hardly be more than an individual character, as we find all degrees of difference in the relative sizes of the two lateral digits in the smaller species.

In some specimens the two lateral digits are of the same size, in others subequal with the ivth slightly the larger and in others this digit is very much larger than ii. One individual exhibits the very peculiar character of having the lateral metapodials of the same size on one foot, while in the opposite foot the fourth metatarsal is much larger than the second.

Metatarsal ii is slightly less reduced than in the average individual of *M. bairdi*. Proximally it bears a large concave facet for the meso-cuneiform and posteriorly there is a small facet by which it abuts against the inferior retroverted edge of the ento-cuneiform. This latter extends

both above and below the meso-cuneiform and conditions the shape of the head of M. ii, about one-half of the proximal surface being supported by the meso-cuneiform. Posterior to this facet the proximal surface slopes abruptly downward and presents the above-mentioned facet. About two-fifths of the internal surface of ecto-cuneiform is taken up with a facet for metatarsal ii, which in *M. bairdi* extends upward proportionately less on the ecto-cuneiform. The shaft is of about the same dimensions proportionately as in *M. bairdi* and was closely applied to M. iii proximally, but both the lateral metapodials curve outward distally. The distal end is merely an enlarged copy of that of the smaller species, is high and compressed and the median keel is strongly developed. Metatarsal iii bears about the same relation to the lateral metatarsals in size as in *M. bairdi*. In the latter we have a distinct facet on M. iii, either lateral or proximal for the cuboid, but in the new species M. iii does not touch the cuboid and the only facet on exterior surface of the proximal end is that for M. iv. It is borne entirely by the ecto-cuneiform and is quite large in proportion to the size of the lateral digits and supports nearly all the weight and receives most of the impacts and strains of the foot. The distal end is somewhat wider than the proximal end. M. iii is quite a little longer than the lateral metatarsals, more so than in *M. bairdi*. All the phalanges are slightly more massive proportionately than in the smaller species.

The pelvis in the Am. Mus. Collection referred to *M. copei*, I do not regard as Mesohippus at all because it is too much specialized in its own way to belong to a White River equine. It differs very much from that of *M. bairdi* and in some respects is more specialized than that of the modern horse. If the reference to *M. copei* is correct, we have in this species a very aberrant side line of the horse series. The pelvis under discussion differs from that of *M. bairdi* in the following respects: (1) The ilium expands very abruptly, almost directly in front of the acetabulum, while in *M. bairdi* it expands very gradually and begins its expansion a long way in front of the acetabulum (see Pl. XIII and Fig. 4). (2) The angle of the ilium in *M. bairdi* and of all the known equines is sharp, but in this specimen it is very much rounded. (3) The crest is broad and stout instead of being narrow and elongate as in *M. bairdi*. (4) The border between angle and crest is very much less concave than in *M. bairdi* and the horse. (5) The border of bone above acetabulum is drawn out into a sharp crest even more pronounced than in the recent horse. (6) The acetabulum is round as in Hyracodon, not elongate as in *M. bairdi* and the horse. (7) The obturator foramen is broader in proportion to its length than in *M. bairdi*. (8) The ischia turn upward at an angle posteriorly almost as much as in the horse, while in *M. bairdi* the ischium is in a straight line with the long axis of the ilium and does not turn up posteriorly. In view of these great differences I cannot regard the reference to *M. copei* as correct.

In the American Museum there are a series of lumbar vertebræ which

are too large for *M. intermedius*, and their provisional reference to *M. copei* is justifiable. These are very like those of *M. bairdi*, but much larger and more massive. The provisional reference of the two premolars described with the type is also justifiable, as they are too large to pertain to any other known species of horse from the White River. Leaving the pelvis out as questionable, we may say that the remains indicate a very large equine agreeing with *M. bairdi* in most of its characters and yet specialized in its own way so that it is a little off the line of equine descent though most probably developed from *M. bairdi*.

Measurements of M. copei.

	MM.	MM.
Tibia	298	313
Calcaneum, length	82	
Calcaneum, extreme width	30	
Astragalus, length	46	50
Astragalus, width of neck	31	37
Height of navicular	11	
Height of ecto-cuneiform	11	
Length of M. iii	177	189
Femur, distal end width	51	
Width of patellar surface	29	
Extreme length of first phalanx of M. iii	24	
" " second " "	11	
" " ungual " "	29	
Length of M. iv	155	
Phalanx 1 of M. iv	14	
" 2 "	9	
" 3 "	22	

MESOHIPPUS INTERMEDIUS O. and W.

M. intermedius, as the name indicates, stands intermediate between *M. bairdi* of the Oreodon beds and *Mesohippus* (*Anchitherium*) *præstans* of the John Day. It occurs in the Protoceras beds. It is a strange and interesting fact that *M. bairdi* continued on into the time of the Protoceras beds after having given rise to the two species.* A careful study of the principal characters of *M. intermedius* brings out very strongly its relation to the preceding and succeeding species. In all these points it is seen to stand directly intermediate between *M. bairdi* and *Mesohippus* (*Anchitherium*) *præstans* of the John Day. In the light of present knowledge there can be no doubt that *M. bairdi* is the direct ancestor of the modern horse, and by the study of the individual variations of the

*A remarkable instance of the persistence of an ancestral type is seen in the Loup Fork. Here Protohippus, a form with long-crowned, cement-covered molars, represents the main line of equine descent, while right alongside of it there is a much smaller species of *M. bairdi* type which Cope has called *Anchitherium ultimum*. This form has short-crowned molars, without cement.

former we can trace a tendency toward the establishment of the *M. intermedius* type.

The skull of *M. intermedius* is much more equine in character than that of *M. bairdi*. It presents the following differences which may be looked upon as modernizations: (1) Increase in length, size and in general proportions. The largest skull of *M. bairdi* observed measures 218 mm., while that of *M. intermedius* measures 280 mm. (2) The upper incisors are all pitted (see Fig. 6), while in the smaller species only the two outer pairs have the enamel invagination. (3) The facial region of the skull is more elongate and the orbit is shifted backward. In *M. bairdi* the anterior border of orbit is over M. 1; in *M. intermedius* it is over interval between Ms. 2 and 3. (4) The diastema between Pm. 1 and the canine is proportionately greater in the larger species.

Fig. 6.

SUPERIOR INCISORS AND CANINE OF M. INTERMEDIUS, ½.

The canine has a well-developed cingulum on its internal surface. This is the foreshadowing of the cupping, as the pit in an incisor tooth is formed by the cingulum, which rises up on the internal border of the tooth to enclose the depression. Teeth have been observed from the lower Oreodon beds which have a strongly developed cingulum anticipating the development of the pit. (5) The occiput is slightly more overhanging in the larger species. (6) The aveolar border of the jaw is better developed and higher in *M. intermedius*. This, of course, is correlated with larger teeth, with longer roots. (7) The postorbital processes are better developed, more nearly enclosing the orbit. (8) There is in *M. intermedius* a large deep antorbital fossa or depression occupying nearly all of the lateral wall of skull and extending forward almost to Pm. 1. (9) The teeth of the molar series are much larger, longer and more specialized than those of *M. bairdi*. These differences, which have been given by Osborn and Wortman in their description, are: (*a*) "The internal cingulum of Pm. 1 is more strongly developed and a distinct basin is formed. (*b*) In the second upper premolar, the parastyle or antero-external buttress is considerably larger than in *M. bairdi* and gives to the crown an incipient triangular shape. (*c*) The midrib of the external lobes is better developed than in *M. bairdi*, and the postero-transverse crest is more nearly confluenced with outer wall of tooth."

Length of Molar-Premolar Series.

M. bairdi....	73.5	*M. intermedius*....	97	*M. præstans*....	112.5

Molar Series.

23	46	51

Premolar Series.

42	53	61

THE MILK DENTITION.

In the Princeton Collection there is a skull bearing the temporary dentition (No. 11168). In the young skull the anterior border of the orbit is just between D. 4 and M. 1, so that as growth takes place the orbit is forced to retreat by the elongation of the facial region of the skull, as in the adult skull the anterior border of the orbit is over the interval between molars 2 and 3. The milk teeth agree in all essential points with those of *M. bairdi*.

Measurements of the Superior Milk Teeth.	MM.
Length milk series	57
D. 1	10
" 2	18
" 3	16.5
" 4	17

The lower teeth of the deciduous set agree in all their characters, except size, with those of *M. bairdi*.

There is nothing noteworthy about the vertebræ except their increase in size over those of *M. bairdi*. The limbs bear the same general proportions as in the smaller species. The scapula is higher and narrower proportionately than in *M. bairdi*. All the limb bones are characterized by being much longer than in the smaller species. The ulna is not more reduced distally than in *M. bairdi*, and is distinct from the radius throughout. The shaft is compressed laterally and is very slender, but distally it is stouter and has a large facet for the cuneiform. Proximally the olecranon is more massive than in *M. bairdi*. The radius is very large and is fast becoming the important bone of forearm. The carpus presents no important differences from that of the smaller species. It is still high and narrow. A rudiment of the fifth metacarpal still persists, but is not so elongate as in *M. bairdi*, but is shorter and stouter and on the way to disappearing. The lateral digits are usually more flattened than in the smaller species but are not more reduced, the distal ends being even more massive proportionately. The ungual phalanges of the lateral digits are long, narrow and sharply pointed at the ends. That of metacarpal iii is proportionately wider than that of *M. bairdi*.

	MM.
Length of M. iii	155
" M. iv	138
" M. ii	143

The ribs are characterized by their length and extreme slenderness, those of the median dorsal region being especially long, not much flattened, being almost round in cross-section. The pelvis presents few characters that are new. The ilia expand even more gradually than in *M. bairdi*. The angle rises up in a pointed process. The crest is partly

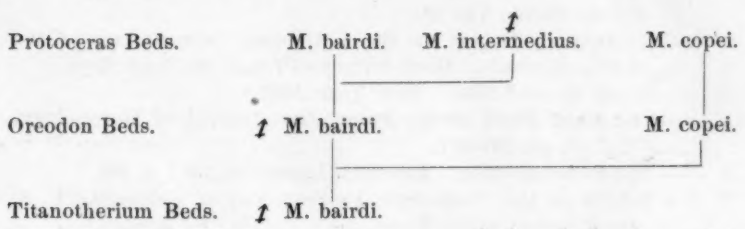
broken away so that all its characters cannot be determined. The border of bone above the acetabulum is rounded and not sharp. The ischia turn upward slightly posteriorly and form more of a plate posterior to the obturator foramen posteriorly than in the smaller species. The sacrum has five vertebræ entering into its formation. The spines of the lumbars are still very high, but they have a more considerable antero-posterior extent proportionately than in *M. bairdi*. The femur has a massive proximal end, the great trochanter being lower and more massive than we usually see it in Mesohippus, but this may in part be due to the fact that our skeleton is of a young animal.* The tibia of *M. intermedius* is somewhat stouter in proportion to its length than that of *M. bairdi*. The cnemial crest is strong and well developed. As usual, there is a large fossa external to the cnemial crest. The fibula is still complete and is distinct from tibia. The proximal end is quite small and the shaft is very much reduced, while the distal end is quite large, forming the external malleolus to articulate with astragalus and with calcaneum in extreme extension. Both proximal and distal ends, as well as the shaft, are closely applied to the tibia, but are not coössified with it. The tarsus of *M. intermedius* is more modern than that of *M. bairdi* in that the tarsus is wider and lower, which is a step in the direction of the modern horse. The calcaneum is very long, the tuber proportionately longer than in *M. bairdi*, and is quite stout with an expanded free end. The cuboidal facet is long and narrow, almost crescentic in shape and extends downward and inward to the sustentaculum. There is quite a large fibular facet. The astragalus is broader and the trochlea is not so deeply incised as in *M. bairdi*, though it is distinctly equine in pattern. The two condyles of the astragalus are very unequal in size. The inner almost always overlaps the navicular facet, while the external is separated from it by a long interval. In *M. bairdi* the internal condyle never reaches the navicular surface. The navicular is much flatter and lower, as is also the ecto-cuneiform, than in *M. bairdi*. The cuboid is also shortened, just equaling the height of the two contiguous bones. metatarsal iii extends over on cuboid.

This is another modernization. There is a distinct facet on the calcaneum for the navicular. There is a much more complete interlocking of the tarsal bones in *M. intermedius* than in any other White River horse. The ento-cuneiform as usual is high, extending both above and below the meso-cuneiform which is still not so deep as the ecto-cuneiform. On its posterior surface it bears a distinct facet for the cuboid with which it unites in forming the small facet for M. iv. Metatarsal iv is usually less reduced proximally than M. ii, but tapers to about the same size distally. This demonstrates the manner in which the reduction of digits takes place in the family. We know from *M. bairdi* that M. i first disappeared and afterward M. v. The condition in *M. intermedius* indicates that M. ii would next become rudimentary, and then M. iv. In the horse where the lateral metapodials are mere splint

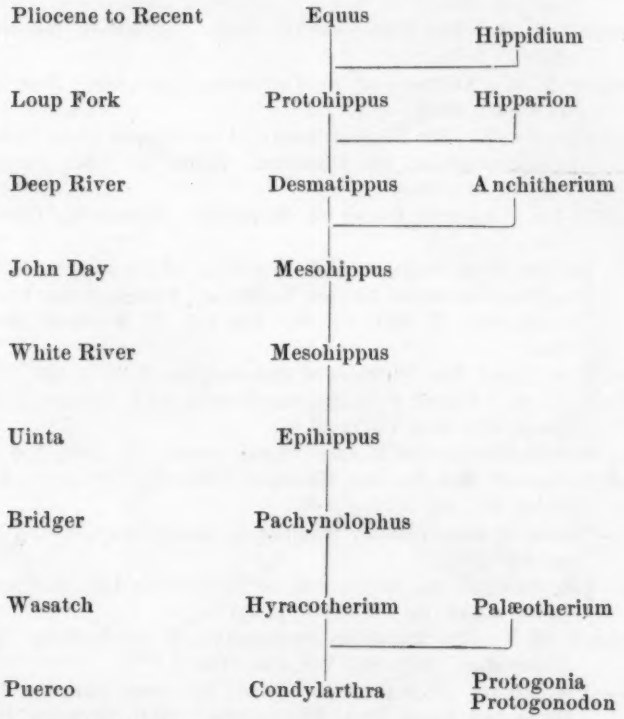
*This may also account for the fact that fibula is not coössified with tibia.

bones and closely applied to M. iii, M. iv is still larger than M. ii proximally.

The inter-relationships of these three species may be expressed by the following diagram:



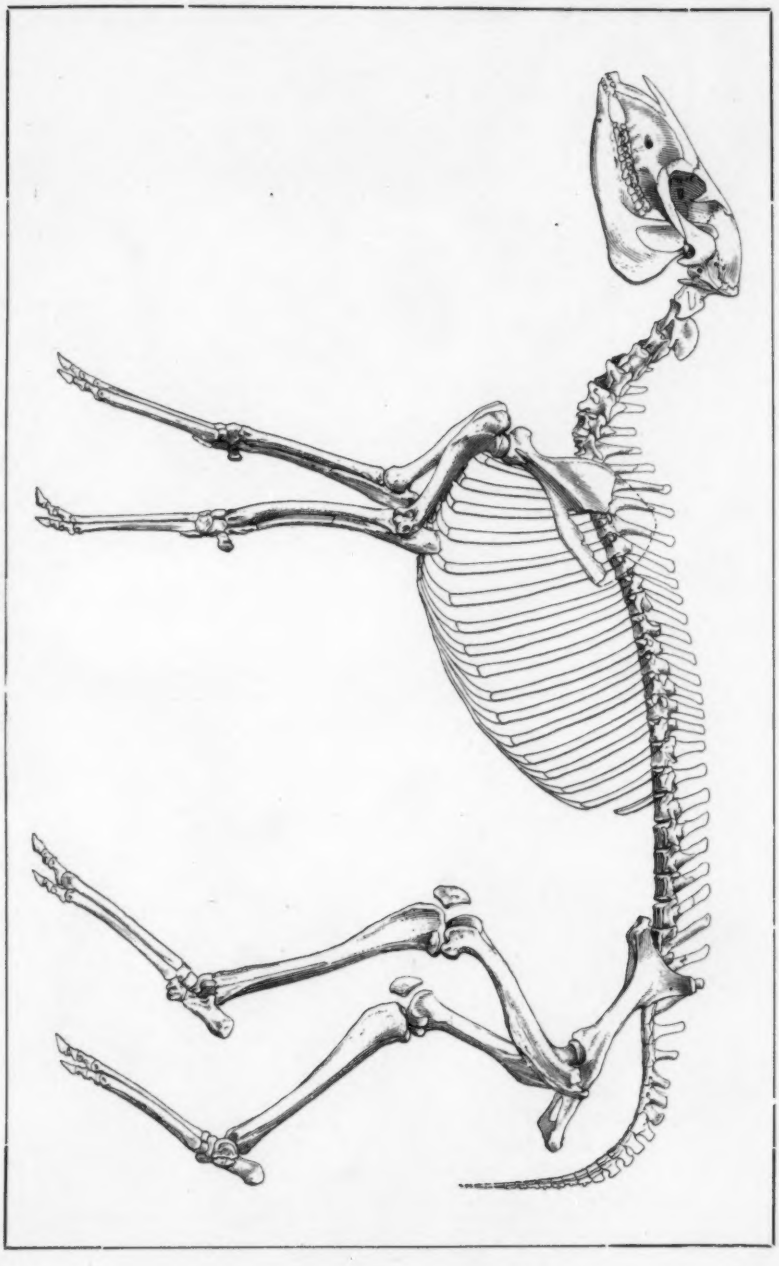
The phylogeny of the horse series as it is now generally understood may be given as follows:



↕ Represents the line of descent.

Literature.

1. Chauveau: Anatomy of the Domesticated Animals. New York, 1873.
2. Cope, E. D.: Tertiary Vertebrata. Rep. U. S. Geol. and Geog. Survey of the Terrs., Vol. iii.
3. —— Preliminary Report on the Vertebrate Palæontology of the Llano Estacado. Geol. Survey of Texas, 4th Ann. Rept.
4. —— Origin of the Fittest. New York, 1886.
5. —— The Hard Parts of the Mammalia. Journal of Morphology, Vol. iii, pp. 137–277.
6. —— The Perissodactyla. American Naturalist, 1887, p. 985.
7. —— Report on the Vertebrate Palæontology of Colorado. U. S. Geol. Survey of the Terrs., 1873.
8. Dana, J. D.: Manual of Geology. New York, 1894.
9. Flower, W. H.: Osteology of the Mammalia. London, 1885.
10. Flower, W. H., and Lydekker, R.: Mammals Living and Extinct. London, 1891.
11. Hatcher, J. B.: The Titanotherium Beds. American Naturalist, 1893.
12. Huxley, T. H.: Anatomy of the Vertebrated Animals. New York (London), 1871.
13. Kowalewsky, W.: Sur l'Anchitherium Aurelianense et sur l'histoire palæontologique des Chevaux. Mem. de l'Ac. imp. St. Petersb., xx, 1873.
14. Leidy, Jos.: Ancient Fauna of Nebraska. Smithson. Contrib., 1852.
15. —— Extinct Mam. Fauna of Dak. and Neb. Philadelphia, 1869.
16. —— Contributions to the Extinct Vertebrate Fauna of the Western Territories. P. 251, Pl. vii, Rep't I, U. S. Geol. Survey Terrs.
17. —— Proc. Acad. Nat. Sciences of Philadelphia, 1850, p. 122.
18. Marsh, O. C.: Polydactyle Horses, Recent and Extinct. Amer. Journ. Sc., 1879, Vol. xvii.
19. —— Recent Polydactyle Horses. Amer. Journ. Sc., 1892, Vol. xliii.
20. —— Notice of New Equine Mammals from the Tertiary. Amer. Journ. Sc., vii, 1874, p. 247.
21. —— Notice of New Tertiary Mammals. Amer. Journ. Sc., Vol. ix, pp. 239–250.
22. —— Introduction and Succession of Vertebrate Life in America. Amer. Journ. Sc., Vol. xiv, p. 337.
23. Osborn, H. F.: The Rise of the Mammalia in North America. Proc. Amer. Asso. Adv. Sc., Vol. xlii, 1893.
24. —— Preliminary Account of the Fossil Mammals from the White River and Loup Fork Formations. Bull. Museum Comp. Zoöl. Cambridge, Vol. xvi.



Restoration of Mesohippus Bairdi, ⅓.

25. —— Mammalia of the Uinta Formation. Pt. iii: The Perissodactyla. Pt. iv: The Evolution of the Ungulate Foot. Trans. Amer. Philos. Soc., 1889.
26. Osborn, H.F., and Wortman, J. L.: Fossil Mammals of the Lower Miocene White River Beds. Bull. Am. Mus., Vol. vi, pp. 199–288.
27. —— Perissodactyls of the Lower Miocene White River Beds. Bull. Am. Mus., Vol. vii, pp. 343–375.
28. Schlosser, M.: Beiträge zur Kenntniss der Stammesgeschichte der Hufthiere. Morphologisches Jahrbuch, 1886, Bd. xii.
29. Scott, W. B.: On the Osteology of Mesohippus and Leptomeryx. Journ. of Morph., Vol. v, No. 3.
30. —— Evolution of the Premolar Teeth in Mammals. Proc. Acad. Nat. Sci., Philadelphia, 1892.
31. —— Mammalia of the Deep River Beds. Trans. Amer. Philos. Soc., Vol. xvii.
32. Wortman, J. L.: On the Divisions of the White River or Lower Miocene of Dakota. Bull. Am. Mus. Nat. Hist., Vol. v, pp. 95–106.
33. Zittel, K.: Handbuch der Palæontologie. Band iv: Mammalia. München und Leipzig, 1893.

On Natural Selection and Separation.

By Arnold E. Ortmann.

(*Read before the American Philosophical Society, May 15, 1896.*)

I. It is generally understood that the chief merit of Darwin in creating his theory of the origin of species is the establishment of the principle of Natural Selection, and that by the introduction of this principle the process of development of organic nature from the conditions existing in former times to the present may be made intelligible, and mostly it is also understood, that natural selection is only one of the factors playing a part in the formation of species. But the proper line of action of natural selection, as conceived by Darwin, is estimated by some other authors very differently. I refer especially to Weismann, who calls natural selection "all-sufficient," which implies that it is the only factor that forms species; but I regard this expression only an exaggeration, since Weismann contradicts himself in this respect.* The assertion, however, stands, that natural selection of itself *may* form different species. On the other hand, Eimer maintains, in opposition to Weismann, that there is

* See Ortmann, *Grundzüge der marinen Tiergeographie*, 1896, p. 30.

no formation of species by natural selection, but that the only action of this factor consists in the preserving of existing species.* This opinion is as erroneous as that of Weismann, but in the opposite direction.

So far, however, Darwin's definition of natural selection, as the survival of the fittest, was not altered, only the efficacy was regarded differently. But recently Pfeffer† has given another conception of natural selection, differing from Darwin's. According to the latter, by the struggle for existence the fittest are selected (hence the term "selection"), while all others are destroyed. Pfeffer, however, says that there is no selection of particularly good variations, but the struggle for existence destroys indiscriminately fitted and not fitted individuals, and certainly it destroys all the not fitted. Thus the surviving remainder (according to Darwin's terminology the selected part) consists of a number of good and better individuals, which show a *good average*. The struggle for existence continued in this way during many generations—destroying all the bad individuals—effects little by little that this good average improves from generation to generation. Pfeffer calls this process "Transformation of species by self-regulation" ("Umwandlung der Arten durch Selbststeuerung").

This conception of natural selection differs only slightly from that of Darwin, and one could say, that only the form of expression is different, while the effect in both cases is the same. But we shall see below, that the form used by Darwin is in some respect inferior to that used by Pfeffer, and although Darwin's meaning is nearly the same as that of Pfeffer, we shall have some advantage in accepting Pfeffer's phrase, especially in maintaining, that not the fittest, but good individuals survive, and that the change effected is an extremely slow one.

Recently I have pointed out,‡ that this "transformation of species" is nothing else than the well-known "mutation" of palæontologists, a term, the differences of which from "variation" are first shown by Waagen and Neumayr, and subsequently most vigorously maintained by W. B. Scott.§ These differences are neglected by many zoölogists, although the "comparatively lawless and uncontrolled character"‖ of the variations and the "directness of advance towards the final goal"¶ of the mutations differ strikingly. Scott says:** "While variations are due to the union of changing hereditary tendencies, mutations are the effect of dynamical agencies acting long in a uniform way and the results

* Eimer (*Die Artbildung und Verwandtschaft bei Schmetterlingen*, ii, 1895, p. 33) uses even the expression: "Inefficiency of Natural Selection" ("Ohnmacht der Naturzüchtung")

† Pfeffer, "Die Umwandlung der Arten, ein Vorgang functioneller Selbstgestaltung," *Verhandl. Naturw. Ver. Hamburg* (3) i, 1894.

‡ *Grundzüge der marinen Tiergeographie*, p. 31.

§ Scott, "On Variations and Mutations," *Amer. Jour. Sci.*, 48, 1894, pp. 355–374.

‖ *l. c.*, p. 370.

¶ *l. c.*, p. 360.

** This sentence is first given in the paper "On the Osteology of Mesohippus and Leptomerys," *Journ. Morphol.*, v, 1891, p. 388, and repeated *l. c.*, p. 372.

controlled by natural selection." If thus mutation is influenced by natural selection, it implies, that any particular mutation must advance in a direction advantageous for the respective species, and, indeed, many examples of mutation known among fossil animals are apparently due to the advantage produced by the change.* I must add here, however that probably not all mutations (in a palæontological meaning) are due to natural selection, but that many do not imply an actual improvement. In this respect Eimer's investigations of the Papilionidæ are important. The variations in the colors of the wings, on which Eimer exclusively relies, are apparently neither useful nor injurious, yet they are caused most likely by external conditions, for example, by warmth or cold during the development of the imago from the larva. Eimer points out, that in his butterflies a distinct direction of variation is evident, which he calls "Orthogenesis." We shall see below that this is a process of inheritance. By the constant action of certain external causes upon subsequent generations, and the repeated inheritance of the characters thus acquired, a certain tendency of variation in a distinct direction may develop. If this tendency does not bear on utility, the degree of variation in the single individuals differs considerably, and even individuals varying in other directions are preserved. Thus a gradual transition results from the less to the more changed individuals. But altogether, from generation to generation, the variation in that direction increases, and the changed individuals may become the most numerous, thus effecting a slow change of the average characters of the species, which looks exactly like a mutation. We may call this latter mutation, produced by accumulative inheritance, by Eimer's term "orthogenesis," in contrast to the "mutation" produced by natural selection. "Orthogenetic mutations" are also known among fossil animals, and I refer† especially to the group of Ammonites whose mutations have been first studied. Here most of the characters advancing in certain lines, ornaments and form of the shell, etc., are apparently not subject to natural selection. Of course, we do not know, in most of the cases, whether a particular transformation is useful or not, and in many cases, where we cannot recognize any advantage, the latter is present nevertheless. But since Eimer's investigations have amply proved that such changes, indifferent as regards utility, are certainly present in living animals, they must also have been present in fossil animals.‡

*I mention only the example of the transformation of the structure of the extremities in the horse-phylum, as discussed by Scott (*l. c.*, p. 368). With the change of one character in a useful direction the change of others may be connected, which are in correlation with the first. This would be an indirect action of natural selection."

†A very illustrative example of "Orthogenesis" is the transformation of the Miocene and Pliocene *Fulgur contrarius* into the Pliocene and Recent *Fulgur perversus*. See Leidy, "Remarks on the Nature of Organic Species," *Trans. Wagner Free Inst. Sci.*, II, 1889, p. 51ff., Pls. 9 and 10.

‡Weismann indeed denies, even in respect to Eimer's butterflies, that there are any useless variations, but this is one of his many assertions, which he does not even try to establish properly (comp. "Germinal Selection," *The Monist*, Vol. 6, No. 2, Jan., 1896,

We cannot say, however, that animals subject to orthogenesis are not at all under the influence of natural selection: the latter must necessarily act also upon them, since all injurious variations are destroyed and cannot be transmitted and give cause to orthogenetic mutations. Natural selection does not invariably imply mutation, but often, especially if the external conditions are unchanged, it effects only a *preservation* of an existing species: by destroying all bad individuals it maintains the good standard of the characters of the survivors, and only if there is any advantage in any variation, this standard will be improved in a direction indicated by this advantage. Thus we may say that natural selection gives origin to mutation in a useful direction, but that this mutation is very slow, and often so infinitesimal, that it amounts almost to nothing, that is to say, only the good standard is saved. This action of natural selection effects besides the general adaptation of each animal form: the surviving individuals comply with the requirements of the surrounding conditions of life.

We have no reason to look upon natural selection as a factor of minor importance, as Eimer is inclined to do. Even the preserving of a good standard is all-important. Natural selection is a factor which cannot be left aside, and which is a necessary one in the development of all beings, and it is a grave mistake to abate its value in favor of any other factor coöperating in the formation of species.

II. Yet the value of natural selection has not only been underrated by some authors, but, on the contrary, it has been overrated, especially by Weissman. The latter believes that natural selection does form species. One can hardly understand on what grounds he is induced to allege this action, and why he even believes that it is the only factor in the formation of species, since he himself accepts Darwin's conception of this factor, namely, that it acts selectively upon the best variations, and destructively upon all the others, thus inducing only a change, a transformation of *one* existing form or species into *one* other, but never causing the origin of *divergent* forms or species. This point is so plain, and so beyond any doubt, that only a great logical mistake, and a complete misapprehension of Darwin's theory on the part of Weismann can explain this error. Yet it is perhaps a little difficult, to say precisely, where the fallacy is hidden, and it would be interesting to examine this point more closely.

I have no doubt that this wrong interpretation of natural selection is

p. 254). Weismann's argument as respects this point is the following: Eimer believes to have shown, that there are no advantages for the respective species visible in the different colors of the butterflies: but since I (Weismann) have propounded the theory, that all characters are due to natural selection, the latter must have produced these color markings also, and we must *assume*, that they are or were nevertheless advantageous! Comp. Spencer (*The Inadequacy of Natural Selection*, 1893, p. 49): "He (Weismann) practically says: Propound your hypothesis; compare it with the facts; and if the facts do not agree with it, then assume potential fulfillment, where you see no actual fulfillment."

due to the form in which Darwin has given the definition of this term. I am confirmed in this belief, as the same error is committed again and again. Still very recently, at the last meeting of the German Zoölogical Society, in the discussion following Eimer's discourse, Ziegler* expressed his opinion that no important difference exists between Darwin's natural selection and Pfeffer's; that it is irrelevant whether one says that the fittest is selected, or that the not fitted are destroyed: both processes have the same or nearly the same result, as may be at once understood by an example he quotes from the breeding of races in domesticated animals.

But even this reference to man's selection in domesticated animals, and the unconditional comparison of it with natural selection, is the weak point, and apparently the term "selection" used by Darwin† induced this error. I shall demonstrate here, that both processes, the natural and the artificial, are certainly not identical, although apparently similar, and especially that the final results of both are entirely different. It is true, Darwin himself avoided this mistake,‡ but it was certainly made by subsequent authors, and especially Weismann must have fallen into it, since his odd misinterpretation of natural selection could otherwise hardly be intelligible.

Weismann apparently has reasoned in the following manner. Natural selection effects that individuals possessing certain useful characters are preserved in the struggle for existence, and man's selection in domesticated animals has a similar effect, preserving individuals provided with certain characters desired by the breeder. Consequently both processes are completely identical, with the only modification, that in the first the principle of utility is ruling, in the second the wishes of man. Farther, since in domesticated animals a great number of varieties or races are often obtained from a single original species, and since these races do not differ in their morphological differentiation from natural species, and indeed are perfectly analogous to the latter as regards their relation to the ancestral forms, it was believed that the natural species originated exactly in the same manner, that is to say, since under domestication different races are obtained by man's selection, in nature different species are formed by natural selection. By this argument, I believe, Weismann came to the view, that species are formed by natural selection alone, and although this opinion of the complete parallelism of natural and man's selection is nowhere explicitly given in his writings, we have to infer it.§

*See *Verhandl. deutsch. Zoolog. Gesellsch.*, 1895, p. 129.

†Darwin, *Origin of Species*, 6th ed., 1878, p. 49: "I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection, in order to mark its relation to man's power of selection." Comp. also p. 65, *ibid.*

‡It is well to be noted that Darwin did not commit this mistake, and that he always regarded natural selection only as taking part in the formation of species, but not as the only cause of it. This is already amply demonstrated by Romanes ("The Darwinism of Darwin and the Post-Darwinian Schools," *The Monist*, Vol. 6, No. 1, October, 1895, p. 3ff.).

§I do not know whether I have succeeded in trying to follow Weismann's thoughts, but I confess freely: if he did not reason as I have conjectured above, I am at a loss to understand him at all on this point. But if the latter is the case, I do not think it is a fault of mine.

But if we analyze the action of man in breeding, we shall find that it does not correspond to natural selection, but is more complex, and that accordingly the final result obtained by man is different from that in nature.

The breeder selects from a certain species a number of individuals fitted for his particular intentions. The whole number of individuals of this species is thus divided into two parts: the *selected* and the *rejected*. By natural selection also the individuals of a species are divided into two parts: the *fitted* and the *unfitted*. There seems to be complete analogy, but this is not the case. In natural selection, as we have seen above, the fitted survive, and the unfitted are destroyed. But in man's selection there is a difference: of course, the selected corresponding to the fitted survive, but the rejected corrresponding to the unfitted are not invariably destroyed. On the contrary, they survive too, at least a great number of them. It is not at all in the breeder's power to kill all the individuals not wanted of the species under domestication; he may kill of a particular litter, perhaps of all his stock those not corresponding to his wishes, he may continue this killing during a series of generations, but he never can succeed in destroying all the rejected individuals of the original species with which he deals. On the contrary, this original species will propagate, and will continue to exist beside the new race obtained from it. The result of the breeder's art is a new race coëxisting with the original species.

See the difference. Natural selection preserves only a number of individuals possessing a certain number of useful characters, while all the others are destroyed: it preserves the good standard of the species or may even improve it. Man's selection, however, gives origin to a new race branching off from the original species, which is preserved, too, and may be subject for itself to the action of natural selection or may be domesticated and subject to breeding again. Therefore, it is easily understood, that it is certainly incorrect to look upon natural selection and the art of the breeder as analogous processes, and natural selection cannot be the cause of the origin of different species.

We may, however, safely say that the races obtained by the breeder are analogous to natural species, and we are to examine by what additional factors the complete parallelism of the breeding of races and the formation of different species in nature is accomplished.

Recently* I have endeavored to demonstrate that we are to imagine natural selection supplemented by the process of *Separation* (or *Isolation*), in order to understand the development of coëxisting different species from one original species. The main point in separation is the action of different conditions of life in different localities separated from each other. The descendants of one ancestral form, if separated *under different conditions*, tend to develop separately, and the directions of either mutation or orthogenesis become different in each separated group: another

* *Grundzüge der marinen Tiergeographie*, pp. 31, 32.

average fitted for the particular conditions of life, or another direction of orthogenesis prevails among the surviving individuals of each group, and after a *permanent* separation during a series of generations the changes in each separated group amount to what is called specific differences.

If we compare in this respect the origin of species in nature with the art of the breeder, we see at once that separation is implied in the action of man. The breeder not only selects his material—in so far he complies with the requirement of natural selection—but he isolates it from the other individuals, and farther on, his chief occupation is the repeated application of the same principle in the separated stock of animals and their descendants, namely, the selection only of individuals answering his wishes. This action corresponds exactly to natural selection in isolated localities. Thus the breeder clearly unites two different actions. (1) The selection of particular individuals possessing certain desired characters corresponds to natural selection. But the breeder cannot, or cannot completely, destroy the rejected remainder. (2) Accordingly he directs his chief attention to the isolation of the selected material, in order to secure control over the true breeding in subsequent generations. Since the organisms kept under domestication are mostly amphimixotic,* the breeder must exclude especially the possibility of interbreeding with the outsiders. This latter point, although clearly understood by Darwin† himself, has been overlooked generally. It was forgotten, that beside the material used for breeding, there exists other "raw" material, and that the preservation of the latter constitutes a very important difference from

* As regards the origin of races as well as of species it matters nothing, whether the respective organism is amphimixotic or not (see *Grundzüge*, etc., p. 32). Amphimixis, that is to say propagation by crossing effects equality, the fusion of different characters, and *not*, as Weismann asserts, the appearance of new variations. This law is not only logically evident, but is amply demonstrated by facts. Comp. Darwin, *Variation of Animals and Plants under Domestication*, 2d ed., ii, 1876, p. 62ff., where numerous examples of the equalizing power of crossing are recorded. This question is to be looked upon as finally settled already by Darwin and no doubt in the most convincing manner, namely, by well-established facts. It is extremely unintelligible how Weismann could throw aside all the proofs carefully collected by Darwin and substitute his own ill-founded conception of Amphimixis. I may add here that between the action of Amphimixis and that of Panmixia as accepted by Weismann, there exists a grave logical error. Amphimixis is the simple process of crossing occurring but once, Panmixia is the same process repeated often and in different directions: the effects of both can only differ in quantity. According to Weismann, however, Amphimix of different animals results in new differences, Panmixia of different animals in the disappearance of existing differences (variations without value for selection are absorbed). This remains an insurmountable contradiction until Weismann demonstrates that his Amphimixis and Panmixia are conceptions contradictory to each other. Eimer (*Entstehung der Arten*, i, 1888, p. 48) says, Amphimixis may produce new things by uniting different things. That is true in so far as the offspring is different from either parent. But this is the first step in uniting the characters of the parents. *The single individuals resulting from the same or similar crossings are more alike to each other than the parents were to each other.*

† Darwin (*Variation under Domestic.*, ii, p. 62) says: "The prevention of free crossing, and the intentional matching of individual animals, are the cornerstones of the breeder's art," and "No man in his senses would expect to improve or modify a breed . . . unless he separated his animals."

the process of natural selection, where such a remnant corresponding to the "raw" material does not survive—unless a *separation* by natural conditions is added.

III. The principle of *Separation* or *Isolation*, first conceived by M. Wagner, is considered by nearly all authors* as a factor of minor importance, although nearly all have conceded, that its occasional action cannot be denied. It was looked upon as an additional factor now and then favoring the formation of species, but not as a necessary one. In the original theory of Darwin isolation is not contained as a particular factor, although Darwin recognized the value of it very well, but he understood it in a purely geographical sense.† As regards the formation of different species he believes‡ it to be explained by the *principle of divergence:* divergence is useful, and if there are any divergent variations within one species, he says (p. 87): "They will be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers." The introduction of this principle, however, is a mere circumlocution of "differentiation of species," not an explanation: we want to know, what are the *causes* of the divergence? If we peruse Darwin's writings in this respect, we find that he was very near to recognizing that separation actually effects the divergence,§ but since he understood separation only in a strictly geographical sense, he failed to put this factor in its proper place. Darwin's principle of divergence is nothing else than the result of separation, and if we substitute the latter for the former we shall complete Darwin's theory in a very important point.

Even Wagner, in introducing the principle of separation, did not give it its correct place within Darwin's theory, but tried on the contrary to replace, at least partly, selection by separation, and farther, he conceived the latter almost entirely in a purely geographical sense. Besides, he laid much stress upon the prevention of the crossing of the separated groups of animals, which is not at all the chief peculiarity of the action of separation. So have all other authors‖ in discussing this principle. But as we have seen, separation acts chiefly in the line, *that each separated group is subject to different conditions of life, and that thus the variations, the directions of inheritance and natural selection become different.* It does not act, however, always in this manner, since separation is possible

*I am to mention that G. Baur is almost the only author who estimates correctly the value of this principle. See the references to his papers: *Grundzüge*, etc., p. 29, footnote, and *Science*, March 6, 1896, p. 361.

† *Origin of Species*, Chaps. xii and xiii.

‡ *Ibid.*, p. 86ff.

§ Darwin (*Origin of Species*, pp. 98–100) uses even the words "confined or peculiar stations," and "isolated stations." On p. 169 he answers the question: "How . . . . can a variety live side by side with the parent species?" by the following: "If both have become fitted for slightly different habits of life or conditions, they might live together" and "the more permanent varieties are generally found, as far as I can discover, inhabiting distinct stations."

‖ For example, Haeckel and Weismann: see *Grundzüge*, etc., p. 31, footnote.

without a change or differentiation of external conditions of life: then a differentiation of species does not result, but we shall have the same species in separated localities. We call such species "relicts" from a former continuous distribution.*

Eimer, although he appreciates the value of geographical separation, names other causes besides: but what he calls "genepistasis" and "kyesamechania" are nothing else than particular actions of separation.

But for a plain understanding we should examine Eimer's theories more closely.†

Eimer‡ defends the opinion that variations are caused by external conditions, but that variability is not an indefinite one, but that the variations are comparatively few, and take place only in distinct directions. There is, according to him, no "fortuitous" or "irregular" variability, but a variability in certain few and distinct lines: he calls this the principle of *Orthogenesis*, and believes that it is contrary to Darwin's alleged supposition of unlimited and "fortuitous" variability. I can hardly see that this difference from Darwin exists at all. It is true Darwin uses the words "indefinite variability," but certainly not in the sense as interpreted by Eimer ("zufällig," "regellos"). Darwin says:§ "All such changes of structure, whether extremely slight or strongly marked, which appear amongst many individuals living together, may be considered as the indefinite effects of the conditions of life on each individual organism, in nearly the same manner as a chill affects different men in an indefinite manner, according to their state of body constitution," etc. That is certainly not a variability subject to casuality, but a variability governed by external causes, which may differ only according to the disposition of the individuals, and this opinion, that "the nature of the organism and the nature of the conditions"‖ are connected in the formation of variations, is also upheld by Eimer.¶

Further, he lays much stress upon the fact that variability advances in a definite direction (orthogenesis), but, I think, he confounds here two actions, that of variation and that of inheritance. Orthogenesis is variation, which is transmitted, and which is accumulated by the repeated action of the *same* external causes upon a series of descendants. We can hardly decide, whether a variation tends to advance in a distinct direction, unless we see that again and again specimens vary in the same direction,

**Grundzüge*, etc., p. 34 and p. 86.

†I go more into details here than seems perhaps necessary, because I consider Eimer's investigations as very important, especially as regards the facts collected. But we shall see that Eimer's views do not differ considerably from Darwin's, and that the chief differences are only differences of terminology.

‡Eimer, *Die Entstehung der Arten auf Grund von Vererbung erworbener Eigenschaften nach den Gesetzen organischen Wachsens*, i, 1888.

§ *Origin of Species*, p. 6.

‖ *Ibid.*, p. 6.

¶Comp. *l. c.*, p. 5. Variation is effected by "Wechselwirkung zwischen der stofflichen Zusammensetzung des Körpers und äusseren Einflüssen."

and if we see the same variation present in different degrees in a large number of individuals, we have reason to suppose that inheritance plays a part, since the amount of change, if often inherited, must on the one hand increase, and since, on the other hand, the force of inheritance is generally different in each individual. Thus orthogenesis, variation in a distinct direction, is the result of the combined action of variation and inheritance: but it is perhaps advantageous to accept Eimer's term, because, as we have seen above, it is important as regards the transformation of species.

Orthogenesis results in series of variations consisting each of a number of individuals varying in the same direction but in a different degree: it unites the single variations into *varieties*, that is to say, into groups of animals showing the same tendency of variation. This grouping of variations into varieties is especially due to inheritance.

Eimer tries farther to find out the causes of the breaking up of any series of variations into *species*, and reaches the conclusion that species are formed when a certain group of individuals within a series "loses its connection with its other allies."* This breaking up of a series of variations in consequence of lost connection he calls "*genepistasis.*"† Under this head come, according to him, *Geographical Separation*, *Halmatogenesis*, and *Kyesamechania.*‡

If we direct our attention to the general definition of "*genepistasis*" given by him, that it is the losing of connection of certain groups, we see at once that genepistasis is exactly the same as separation, and under the same head comes *kyesamechania.*§ The latter term means that a sexual crossing between animals of more or less different characters is rendered impossible by morphological or physiological causes. This impossibility of crossing is certainly not the first *cause* of difference, but it is the *result* of already existing differences produced by beginning separation, and as respects the formation of species, kyesamechania can never be a primary cause of the origin of different species, but it is the result of the beginning differentiation, and may develop an additional factor accelerating the process of specific differentiation.

As regards *Halmatogenesis*, which means the sudden appearance of any new variation, Eimer explains this process by correlation:‖ but this explanation is insufficient. If any character changes, other characters connected by correlation with it change also, but if the change of the first is slow, certainly the changes of the others are so also, and a sudden change of characters by correlation presumes a sudden change of the leading character. Thus correlation cannot explain halmatogenesis.

* See *l. c.*, p. 26: "Wenn . . . . eine Gruppe von Individuen . . . . auf irgend eine Weise die Verbindung mit den übrigen Verwandten verloren hat . . . . spricht man von Arten."

† See *l. c.*, p. 30ff.

‡ I cannot make out with certainty what Eimer thinks as to the logical relations of these terms to each other, but I hope I have quoted him correctly.

§ See Eimer, *Die Artbildung und Verwandtschaft bei den Schmetterlingen*, ii, 1895, p. 14ff.

‖ See *Entstehung*, etc., p. 53.

But we do not need this at all. Halmatogenesis is a well-known process of inheritance, and comes under different heads in that chapter. For example, accumulative inheritance (even orthogenesis) may effect a sudden rise of the degree of development of a certain character, or characters remaining latent during one or more generations may come suddenly into reappearance, or farther, atavism may effect the same. Halmatogenesis does not at all play a part in the breaking up of a "chain of organisms," but it takes part only in the formation of varieties.

Therefore, of Eimer's new terms, only *Genepistasis* and *Kyesamechania* may form different species, and both are nothing else than *Separation*, or as Eimer himself says: "the interruption of connection."

By this brief sketch of Eimer's views we see that there is no considerable difference from Darwin's theory,* except that he considers natural selection to be of minor importance. This is probably due to the fact that he has investigated chiefly characters not at all subject to natural selection. He forgets, however, that even upon animals provided with indifferent characters natural selection must necessarily act in order to maintain the good standard of all the other characters. All the principles introduced by Eimer: Orthogenesis and halmatogenesis as forming varieties in a distinct direction, genepistasis and kyesamechania as forming species, are only new words for old ideas, which indeed have been set forth already by Darwin. And farther, these new terms are mostly results of well-known laws and not the primary causes of the formation of varieties or species, and they do not give us a better knowledge than before of the respective processes, in some cases, indeed, they may even induce confusion.

As respects *separation* we have seen that Eimer considers it only as an additional† factor causing specific differentiation, but farther we have seen that his genepistasis is also separation. Like all the other authors he apparently has conceived separation only in a purely geographical sense. I have, however, demonstrated‡ that we are to conceive the term *separation* in a *bionomical* sense, that is to say, that any causes "effecting a permanent interruption of the bionomical continuity between certain groups come under the head of separation. Separation keeps particular groups permanently under particular conditions, and thus they are prevented from migrating from one station of definite conditions of life into others with other conditions."

* Eimer identifies Darwin's theory with the "Darwinism after Darwin" (comp. *Artbildung und Verwandtschaft bei Schmetterlingen*, ii, 1895, Preface, p. v), in supposing that Darwin's theory alleges that species are formed by natural selection. But we know that this is an entirely unwarranted imputation.

† See *Artbildung*, etc., 1895, p. 9. I should like here to point out an apparent error in Eimer's arguments for the origin of new species in the middle of the range of the original form: he says (*ibid.*, p. 11) that the group of *Papilio asterias* originated from amidst the province of distribution of the group of *P. machaon*. A glance at his tables (Pl. vi–viii), however, shows that this is not the case.

‡ See *Grundzüge*, etc., p. 31, and *Amer. Jour. Sci.*, p. 63, et seq., 1896.

This prevention of migration is very important. *Migration* (as understood by M. Wagner) is an accessory factor, often coöperating with separation, and often working against it. Each species, which originated in a limited area, tends to occupy other territories: it is a well-known fact that each animal form possesses its peculiar "means of dispersal," and by such means it migrates. Migrating species occupy new territories, which have either the same or slightly different conditions of life: in the latter case migration by itself may induce new variations in consequence of the slightly modified action of the external conditions of life. Further, migration is often slow, or only possible under peculiar circumstances, often it is accidental, and only a few individuals can transgress the original limits on rare occasions: then even migration acts as a means of separation. The few individuals occupying a new locality are afterwards practically separated from the original stock remaining in their native country, and thus they may develop separately into a different species, even in the case that immigration from the original stock is not altogether impossible, since any rare individuals of the latter, reaching the new colony from time to time, are soon absorbed by the new form and their characters disappear by the continuous crossing with the modified individuals and by the transforming power of the external conditions. Separation, however, is not always connected with migration: the original "centre of origin" of a species may be broken up again into parts, thus inducing the origin of new species, if the external conditions favor it.

Separation in any form may be more or less complete, and since between complete continuity and complete separation intermediate steps are interposed, also a complete differentiation of species is reached by degrees. This corresponds exactly with what we see in nature. We know of many groups, the species of which are very insufficiently limited and pass gradually into each other: in such cases the formation of species is not yet accomplished. It is an incomplete separation, if a species occupying a large area is divided into different varieties, which are locally more or less limited, and differ in most remote localities considerably, while in intermediate places intermediate forms are present. The distinct varieties on the most extreme limits of the range are certainly under different conditions of life, but in the intermediate area transitions are present: a complete differentiation of species is not yet reached here, and we have to regard these forms still as varieties.

Of course, it is possible, that nearly allied species, which originated separately, may occupy by migration the same territory and come into competition with each other. If their morphological and physiological peculiarities are not sufficiently fixed, there may result by hybridization a new species. But if the characters are well fixed by inheritance, especially if there is "kyesamechania," they may live together or the stronger may suppress the weaker. But I may safely say, that it is very improbable that two closely allied species ever lived precisely under the same conditions in the same locality. I refer in this respect to the example of four

species of the Derapod genus *Gelasimus* on the East African coast recorded by me.* These four species lived in a particular locality completely separated, although often only a few yards from each other, and a collector less careful would have put them all together in one jar. Yet as a rule collectors are well acquainted with the fact that particular species are to be sought for in particular localities.

IV. I may, I think, conclude. I have amply demonstrated that only *separation* can effect differentiation of species, and that all the principles created by other authors for this particular effect come under the head of separation, *i. e*, the breaking up of a number of individuals into groups, each subject to particular conditions of life. Some authors, indeed, have not understood at all that the whole process ending in the formation of species is composed of a series of distinct factors, only the last of which is separation. But I wish to say here expressly that already Darwin conceived those different factors correctly, and distinguished them well according to their particular line of action. The only change of Darwin's views that I should like to propose is to substitute for his "principle of divergence" that of "separation." Besides, it would be well to conceive the term "Natural Selection" in a modified sense, as Pfeffer has proposed, and we have seen that there is some advantage in so doing. And farther, Eimer has pointed out that not all the characters of each animal form are subject to natural selection: there are many which do not bear on utility, but are indifferent in this respect. But since such characters are probably also due to the influence of external conditions, they may be transmitted and may increase, giving origin to a distinct direction of variation,† to a "mutation," which is independent of natural selection, and may be called by Eimer's term "Orthogenesis."

For the rest, the whole of Darwin's theory stands, and none of those "Darwinists after Darwin"—I venture to say—have been able to weaken any of his ideas in the least degree. Especially Weismann has not, since

*See *Grundzüge*, etc., p. 33, footnote. Compare also the following sentences of Petersen (*Det Videnskabelige Udbytte af Kanonbaadens Hauchs Togter*, 1893, p. 455): "Each species seems to be distributed according to certain rules, which . . . . can be brought in relation to one or several . . . . natural conditions," and (p. 457): "no species is found everywhere in our seas," and farther: F. Dahl, "Vergleichende Untersuchungen über die Lebensweise wirbelloser Aasfresser," *Sitz. Ber. Akad. Wiss. Berlin*, January, 1896, pp. 29, 30.

†Already Darwin holds the same opinion and concedes (*Origin of Species*, pp. 170, 171), that there are variations which appear to be of no service whatever to their possessors. This passage is the more interesting, since he talks of the "laws of growth," which are apparently identical with Eimer's "Gesetzen organischen Wachsens." Comp. farther, *ibid.*, p. 175: "When from the nature of the organism and of the conditions, modifications have been induced which are unimportant for the welfare of the species, they may be and apparently often have been transmitted . . . . to numerous . . . . descendants," and p. 176: "Morphological differences, which we consider as *unimportant* . . . . first appeared . . . . as fluctuating variations, which sooner or later became constant through the nature of the organism and the surrounding conditions." (In the last passage the word I have italicized stands originally as *important*, but according to the foregoing and following sentences this is no doubt a misprint)

it is now demonstrated by the ablest scientists explicitly,* and by many others incidentally, that his theories are without any proper foundation. As regards Eimer's theories, I have endeavored in the above to show, that the alleged opposition in certain points to Darwin does not exist, except as Eimer creates new scientific terms for old ideas, and as he does not distinguish properly between cause and effect.

To sum up, we have to distinguish *four factors*† accomplishing the diversity, development and differentiation into species of organic beings: we may call conveniently this whole process: *origin of species.*

1. All organic beings *vary.* There exists an "inherent tendency to vary,"‡ but this tendency is manifested only by the influence of external causes upon the respective organism. The faculty of variation is an unlimited one,§ but the actual variation is limited, namely by the external conditions of life. Variations coming into existence are modifications "directly due to the physical conditions of life," which "in this sense are supposed not to be inherited."‖ *A variation is impossible without external conditions producing it.*

2. *These variations may be transmitted to descendants.*¶ Inheritance is due to the process of propagation, which may be either by *one* parent or by *two* parents (Amphimixis). By inheritance acquired characters are transmitted from the parent to the descendants, and thus the consanguinity becomes morphologically visible, and individuals of common descent are more closely connected by morphological characters with each other than with any other group of individuals. By inheritance the unsteady and temporary variations are transformed into *varieties*, that is to say, into groups of individuals having the same ancestors and resembling each other more or less.**

* I refer to the following names: Eimer, Haacke, Haeckel, O. Hertwig, Pfeffer, Romanes, Spencer, and others. I would especially mention O. Hertwig's book, *Zeit- und Streit-Fragen der Biologie*, Heft i, "Praeformation oder Epigenesis." I recommend this masterpiece of criticism for study, not only because it refutes completely Weismann's fantastic germ-plasma theory, but because the exposition of this theory given in that work is much more intelligible than that given by Weismann himself. In his latest paper ("Germinal Selection," pp. 282, 283 and 286) Weismann refers to Hertwig's criticism: but his remarks are entirely aside from the question, since they do not touch the chief point, and, partly (p. 282), attribute to Hertwig an opinion which the latter, according to his own express statement, did not entertain (see pp. 10 and 11 of Hertwig's book).

† See *Grundzüge*, etc., p. 32.

‡ Darwin, *Var. and Domes.*, p. 2.

§ Unless checked by inheritance!

‖ Darwin, *Orig.*, p. 33.

¶ The transmission of acquired characters is denied by many competent naturalists and cannot be regarded as demonstrated. In the problems of geographical distribution one is continually brought back to this as a probable assumption, and I propound it here as a "working hypothesis."

** Darwin, *Orig.*, p. 33: In "the term variety . . . . community of descent is . . . . implied."

The process of inheritance is most obscure.* We know nothing of the causes of inheritance or—perhaps it is better to say—of non-inheritance often occurring. Weismann's theory of inheritance, even if we accept it (as I do not), does not explain the essence of heredity: it merely refers inheritance to minute processes in fertilization. But this knowledge that heredity is due to the peculiarities in propagation is a very old one, as old as modern zoölogy and perhaps even older, and more accurate knowledge of the minute details in propagation, and their arbitrary augmentation by supposed complications does not promote our understanding of heredity. Yet we do not know how the "tendencies of inheritance" of the germs (or parts of the germs) are transferred to the "soma" of the descendants; we do not know how the germs get these "tendencies" from the "soma" of the parents; we do not know why certain "tendencies" become visible in the descendants, while others do not; we do not know what a "tendency of inheritance" is like anyhow.† A theory of inheritance has to endeavor to answer the questions put here, otherwise it does not explain anything, and the essence of heredity continues to be as obscure as before.

By inheritance and repeated action of particular external conditions a distinct direction of variation may be induced: certain animal forms tend again and again to vary in the same direction, and the degree of the variations is thus increased. This process is what Eimer calls orthogenesis, and if the action of the external conditions as well as of inheritance is not a steady one, but interrupted and irregular, we have his halmatogenesis. Both terms clearly come under the head of inheritance. Orthogenesis and halmatogenesis can effect "mutations," but we must bear in mind that here no principle of utility comes into play.

It is well to be noted that the two factors mentioned, variation and inheritance, act only upon single individuals. They act often upon a number of individuals in the same or analogous manner, but each individual can vary and inherit without regard to others. The two following principles (natural selection and separation) can only act upon a multitude of individuals simultaneously, and their action becomes conspicuous only by the comparison of many individuals.

3. Upon the material produced by variation and inheritance acts a third factor: *Natural Selection.* By this principle all variations injurious in the struggle for existence, all the forms not fitted for existence under a

*See Osborn ("The Hereditary Mechanism and the Search for the Unknown Factors of Evolution," *Biol. Lect. Mar. Biol. Lab.*, Wood's Holl, 1895): "If acquired variations are transmitted there must be some unknown principle in heredity."

†Of course, Weismann has tried to answer these questions, at least partly, by his "theories," but such questions cannot be explained at all by "theories," the very foundations of which are either disputable or arbitrary, or even illogical and contrary to the known facts. On the whole, Weismann's arguments run in a perfect *circulus vitiosus.* His theory of inheritance is founded upon the belief that acquired variations are not transmitted, and the demonstration, that acquired variations are not transmitted, is founded upon the belief that his theory is correct (comp. *Neue Gedanken zur Vererbungsfrage*, 1895, pp. 11 and 21).

certain sum of conditions of life are destroyed. The remnant left is fit for existence, and all the individuals surviving are able to live and propagate. There may be slight differences between them, especially as regards characters not bearing on utility, but a certain average of good characters is present. Natural selection at least preserves this good average, and if there arise any useful characters, a smaller percentage of the individuals possessing the latter is destroyed, and thus the better individuals may gain little by little the preponderance in number: the average is displaced slowly in a distinct direction, namely, toward the better. This latter "mutation" is distinguished from the mutation by orthogenesis by the advantage connected with the particular line in which the change advances. Natural selection effects a general adaptation of the whole number of the surviving individuals to particular conditions of life.

4. But natural selection does not form species; it only preserves or transforms already existing species. If we suppose, however, that of the individuals surviving in natural selection different groups are *separated* from each other under different conditions, and that this *separation* cannot be overcome, so that each group must remain under the constant action of particular conditions, the difference of the latter effects, that each group tends to develop its characters in a different direction. It is true, if upon each separated group the same external conditions act in the same manner, there would be, of course, no separation of the directions of development. But differentiation of the external conditions by bionomic separation, and the splitting into groups of individuals living formerly under the same conditions will give origin to different characters in each group, and animals distinguished by the constant presence of different characters we call *species*. *Different species are formed by bionomic separation; separation does not always imply differentiation of the conditions of life, and accordingly does not always form new species; but if there is a differentiation into species, it is always due to separation under different bionomic conditions.*

In the above the particular action of each of the four chief factors playing a part in the evolution and diversification of the organic world is properly limited. We have seen that the two last-named factors, selection and separation, are imitated by man in the breeding of domesticated animals. Both nature and man use the material furnished by variation, and the success of both is warranted under the condition that the acquired characters may be fixed by hereditary transmission. The four factors named, *variation*, *inheritance*, *selection* and *separation*, must work together, in order to obtain different species, and, indeed, they do so always; it is impossible to think that one of them should work by itself, or that one could be left aside.

The proper action of each of these factors was recognized almost correctly by Darwin, only as respects the differentiation of species, which he attributes to the principle of divergence, he was not quite satisfied.* But

* Darwin, *Origin*, p. 87: "Though it was a long time before I saw how."

most of the successors of Darwin, especially those who pretended to have modified, corrected or enlarged his views in any respect, have not understood his theory correctly: generally the origin of variations, varieties and species has been hopelessly confused, and the latter is especially true of the writings of Weismann, in which the origin of species and varieties, and the origin of the adaptive characters of life are mixed up constantly.*

In, conclusion I should like to add that the principle of separation, as set forth above, bears very importantly on the definition of the systematic term *Species*, and indeed, that it alone enables us to give a correct definition of it. There is no doubt that a proper and logical definition of any term depends largely on the knowledge of the genesis of the object, and in the present case we may say that if the process of the formation of species is properly understood, we can derive from this knowledge a definition of the term species. In my book often above referred to, I have propounded the following:† "*We designate as* SPECIES *such forms as in consequence of* SEPARATION *differ sharply and constantly by morphological characters from allied coëxisting forms.*" It is not necessary that separation should be still evident in all the existing species: the separating causes have often disappeared, while their result, the different species, still exist. But then the separation in the past must have been sufficient to modify and differentiate the respective forms in such a degree that the characters are fixed by inheritance, so that changed external conditions cannot influence them again, and farther, there must be kyesamechania, which prevents hybridization. The possibility, however, of hybridization by artificial means cannot be always regarded as a proof against the value of the respective forms as species: if two species live separated they do not interbreed in nature, and if they are forced to do so, this possibility cannot affect their value as species under normal and natural conditions.

As separation is reached by degrees, distinct species must have developed gradually, and such must still develop. We know numerous examples of so-called "polymorphous" genera, where apparently the process of formation of species is beginning or not yet accomplished. It is true, variations, varieties, and species pass gradually into each other, but this does not imply that these three terms shall be treated alike, and that there is no difference at all between them. A tree is not a shrub, although there are intermediate growths. So we can give a correct definition of variety and species, although there are intermediate forms, which may be doubted, whether they belong to the one or the other.

* This confusion of Weismann's ideas is most evident in the two last pages of his latest publication ("Germinal Selection," *The Monist*, Vol. 6, No. 2, January, 1896, pp. 292, 293). This whole paper is devoted to the demonstration of the action of natural selection as effecting *adaptation*, and though he says that "the mode of formation of the living world as a whole" may be understood by this principle!

† See *l. c.*, p. 32.

The principle of *constant difference* is practically applied generally by systematists, and I hope I have given above a logical foundation of this principle. In many cases, indeed, the constancy of difference is the only means by which species can be distinguished, if the former or the actual separation of the respective forms cannot be made out with certainty. But in all cases, where an actual separation is evident, we should consider the respective forms, if morphologically distinct, as species, not as varieties. Under the new definition of the term species given here, many of the so-called local varieties become species, since such are often distinguished only because the differences from "good" species are only slight ones and are not considered as important enough to create a distinct species. But this standpoint is not correct: any difference in characters, however slight, constitutes a distinct species, if constant and due to separation.